Ecological Thresholds as Constraints to the Growth and Survival of Woody Tree Species in Degraded Grassland in the South Island's Dryland Zone

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Abstract

The native dryland zone in New Zealand's South Island has been drastically altered by burning, grazing, and other anthropogenic activities since human first arrived some 700 years ago. Only 30% of its original native vegetation remains, with <2% of it legally protected. Preserving what is left of the remaining natural ecosystems is urgent, and ecological restoration can be an important part of the solution to increase the area by reclaiming some of the degraded landscape within the dryland zone. However, reintroducing native plants as seedlings is mostly ineffective if disturbances have pushed ecological processes over certain thresholds that now represent barriers to ecological succession and restoration. These ecological thresholds can be the exposure of seedlings/saplings to direct sunlight and strong winds, water stress, soil compaction, herbivory, or competition between the native and exotic species for resources, among others.

The objective of the research described in this thesis was to identify management interventions that might allow restoration to overcome key ecological thresholds preventing the establishment of native woody vegetation. The research was undertaken at five study sites in Northern Canterbury and the Mackenzie Basin. A combination of ground cover manipulation and shading trial, together with irrigation and grazing exclusion, were used to investigate the options to overcome these thresholds for the establishment and growth of native woody tree species. The results showed that the native seedlings had higher probability of survival and growth rates in the shaded treatments, likely due to increased soil moisture and soil aeration. Removal of exotic grasses, irrigation, and fencing also increased native seedling establishment; however, the best results were detected when these treatments were combined with shade. Therefore, ecological restoration of degraded dryland areas on former agricultural/pastoral lands can be achieved if the effects of direct solar radiation on soil aeration, soil moisture, and microclimate are reduced through the creation of shelter for planted native seedlings. Additionally, exotic plant species must be removed, or at least reduced in density, and herbivores excluded in order for restoration efforts to be more successful.

To my parents, Carlos Alberto and Oscarina Rodrigues, and my dogs: Monica, Hulk, Bolacha, Agatha, Abgail, Thor, Ziggy, Grafitte, and Rocky.

"To be poor and be without trees, is to be the most starved human being in the world. To be poor and have trees, is to be completely rich in ways that money can never buy."

— *Clarissa Pinkola Estés*, The Faithful Gardener: A Wise Tale About That Which Can Never Die.

1. Introduction

The dryland zone in the South Island is one of the most altered native ecosystems in New Zealand, with only 30% of its original native vegetation remaining (Rogers et al., 2005). The natural vegetation cover of the dryland zone has been drastically reduced due to burning, grazing, cultivation and other anthropogenic activities. Even where native vegetation remains, human-induced fire and other disturbances have continuously altered this ecosystem (Wilmshurst et al., 2007). The long history of agricultural activities and grazing in this landscape means that soils have often become compacted or somehow degraded, and soil moisture properties have most likely changed (Payne & Norton, 2011). As a result, regeneration of the native vegetation is often difficult in abandoned farmland because of modified environmental characteristics which impose active management of restoration efforts to ensure successful establishment of the plants. Walker et al. (2009b) suggest that it is possible to change the vegetation community from a less degraded state to a woodier component if disturbances are reduced or eliminated and seed sources are available. They also suggest that these communities can gradually (and slowly in drier sites) move on to a taller woody community over time. Rose et al. (2004) and Rose & Frampton (2007) support the hypothesis that transitions may occur depending on seed availability, site conditions (e.g. soil properties, climate) and species traits.

Plants are usually able to recolonize a degraded area once disturbances cease (Arnold et al., 1999; Walker, 2000; Maza-Villalobos et al., 2011). However, natural succession does not initiate on some sites even after disturbances are removed (Holl et al., 2000; Standish et al., 2007). Natural regeneration can be especially limited in areas where the general landscape has lost all of its soil cover (e.g. mining sites), or where the soil has become compacted or toxic for plant growth (e.g. intensive pastoral and agricultural activities). Additionally, the loss of seed bank and other propagule sources can also prevent or retard natural regeneration (Yates et al., 2000; Wardle et al., 2001; Zhao et al., 2005; Measham, 2009; Tang et al., 2009). Hence, identifying the potential environmental conditions that might be affecting natural vegetation succession and

hindering restoration efforts has become the main subject of interest for restorationists (Standish et al., 2009). How can the lost ecosystem be restored more quickly so that environmental services may function again? Furthermore, in cases where natural succession does not occur anymore, what can be done to initiate it? Degraded landscapes that have undergone disturbances that led to modifications in the ecological processes and, therefore, no longer support the native vegetation may require active intervention of restorationists to overcome specific environmental barriers (biological and/or abiotic conditions) in order to promote and guarantee restoration success (Hobbs & Norton, 1996; Hobbs & Harris, 2001; Standish et al., 2009). Understanding what these barriers or ecological thresholds are will enable restoration ecologists to determine the methods and tools to restore degraded ecosystems more effectively (Mullineaux et al., 2003; Suding & Hobbs, 2009).

New Zealand's dryland zone is one of the country's most endangered ecosystems and is also the least well protected (Walker et al., 2009b). Therefore, the need to expand and increase the current area size of native dryland in New Zealand is fundamental for the maintenance of this ecosystem's biodiversity, along with protection of soils and waterways. Change of land tenure has raised the interest of conservationists in using formerly agricultural and pastoral lands for this purpose. However, natural succession and restoration efforts seem limited on these lands as a consequence of changes in the environmental characteristics of the sites after decades of farming. The focus of this research was to better understand some of these environmental constraints to restoration efforts, henceforth called "ecological thresholds", and how they can be manipulated to enhance restoration success on former agricultural lands. A combination of ground and aboveground treatments was established on five study sites in Northern Canterbury and in the Mackenzie Basin, for the purpose of testing grass removal effect (Rank Grass trials), supplemental water (Irrigation trial), herbivory (Grazing trial), and shade on the establishment and growth of native woody tree species.

The following pages, a schematic description of the disturbance pathways that led to the degradation of New Zealand's dryland zone is presented in Section 1.1 (Diagram). The General hypotheses section presents the questions around the ecological thresholds manipulated in the two experiments (Rank Grass and Degraded Short Tussock trials), how their manipulation was expected to affect the current environmental conditions, and the responses from the native

seedlings. The Literature Review section contains a bibliographic review of the current degraded state of New Zealand's dryland zone and of the necessity to increase the conservation status of this ecosystem through restoration of abandoned farmlands. The approach taken was based on the recent theories of ecological succession and state-and-transition models that include alternative states and the development of novel ecosystems as possible scenarios for a regenerating landscape. The theory around environmental thresholds is further introduced and explained, as well as how disturbances in natural ecosystems can transform ecological processes into factors that can potentially restrain the return of the native vegetation or cease succession completely. The list of possible environmental thresholds to ecological restoration is vast; hence, the present research concentrated on current environmental characteristics of the study sites, such as the presence of exotic grasses, soil moisture levels, and intense solar radiation as the main causes of restoration failure on these sites specifically. The effects of herbivory on the native seedlings were only analyzed through one trial (Grazing Trial), whereas all the other study sites fenced off and herbivory was assumed inexistent or insignificant for the analyses. The Methods section presents a description of the study sites, their location, specific restoration issues for each site, and a layout of the experiments. Still in the Methods section, the procedures (field and laboratory methods) to obtain the data for the statistical analyses are described, as well as the construction of the statistical models in a Bayesian framework in order to answer the general hypotheses: what is the probability that native woody tree seedlings will establish and grow under the current environmental condition? Which environmental factor, or factors, is most definitely restraining the persistence of native woody seedlings in these areas? Based on the analyses of survivorship, growth, and physiological measurements presented in the sections 4 and 5 (Results of the Rank Grass and Degraded Short Tussock trials, respectively), the environmental factors that are linked to restoration failure on former farmlands in New Zealand's dryland zone are discussed in sections 4.4 (Rank Grass) and 5.4 (Degraded Short Tussock) based on the literature and other researches. Finally, Section 6 presents the conclusions drawn based on the Rank Grass and Degraded Short Tussock experiments and suggestions are made to overcome the ecological thresholds identified as key environmental factors preventing ecological restoration on these particular study sites, but also in other areas with similar ecological characteristics to the degraded sites analyzed in this thesis.

1.1 Diagram

The diagram in Figure 1-1 depicts the degradation factors (black arrows) that transformed the native woody vegetation of pre-human times in to the current exotic grassland, herbfield and woody vegetation types. The red arrows indicate the possible recovery pathways of the degraded exotic grassland and herbfields back to native woody vegetation if the indicated thresholds (numbers 8 to 11, the focus of this research) are overcome. The green dashed arrows are also pathways to recovery of degraded landscapes, but they are not considered in this study. In this thesis, the ecological thresholds observed in the exotic grasslands and herbfields where the study sites are located will be assessed as to determine whether they are constraints to the regeneration of the woody vegetation in these areas and how these thresholds might be overcome through management interventions.

The degradation factors depicted in the diagram (numbers 1 to 7) can be summarized as follows:

- The dryland zone in the South Island is believed to have been covered by native woody vegetation in pre-human times that was reduced to native grassland by Polynesian/Maori settlers, and later by Europeans, through burning (1);
- The native grassland have been further degraded into exotic herbfield as a result of European agricultural practices, especially overgrazing by livestock usually in combination with invasive animals and exotic herb invasions (hawkweed and browntop). These exotic species were originally brought into New Zealand to improve pasture quality for grazing animals (browntop) or occurred as impurities in seed imports (Hawkweeds) - (4,5);
- The further modification from native to exotic grasslands has been driven by European agricultural practices such as cultivation, fertilizer application and irrigation (3). The same activities also transformed exotic herbfields into exotic grasslands. Exotic grasslands were also created directly by European deforestation, burning and harvesting/felling (1,2), normally followed by sowing and fertilizer application; and more recently, by cultivation and irrigation (3); and
- Both exotic grasslands and herbfields may be transformed into exotic woody landscapes through land abandonment and/or low agricultural input, often followed by the removal of grazing pressure (6), and the subsequent invasion of exotic woody plants (7) especially

conifers (*Pinus* species and *Pseudotsuga menziesii*) and some exotic shrub species (European broom, gorse, hawthorn etc). Native grasslands can also be invaded by exotic woody species under similar situations.

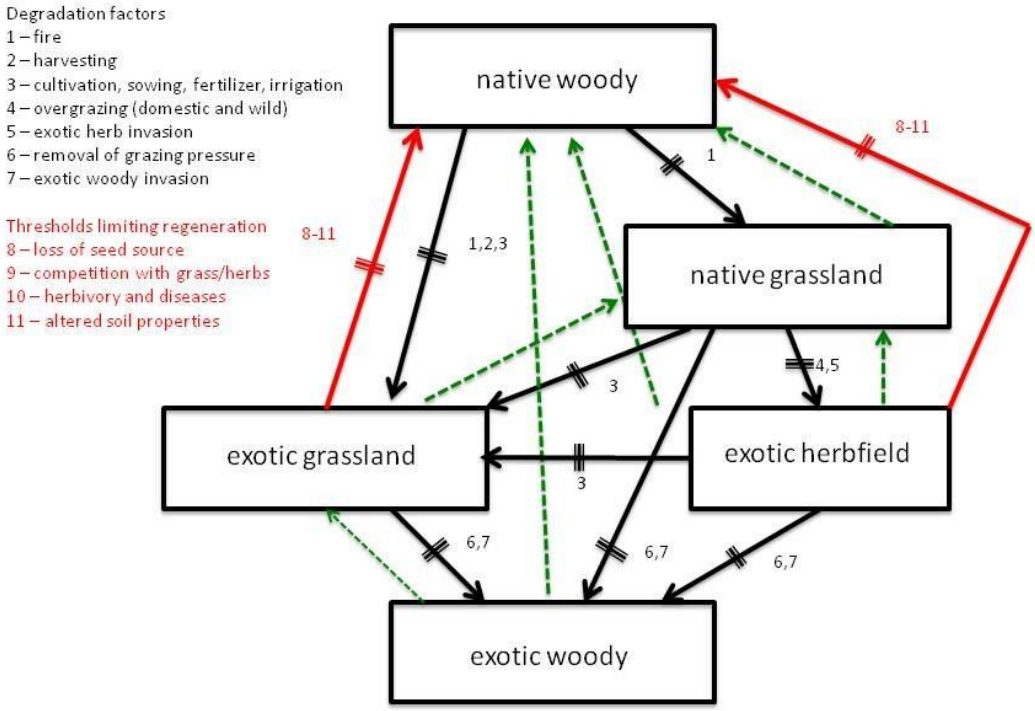


Figure 1-1 Pathways of ecosystem degradation and potential recovery of eastern South Island drylands (dashed green pathways not considered in this thesis).

The focus of this study lies on the pathways to recover/restore exotic grassland and herbfield back to native woody vegetation and is represented by red arrows on the diagram. The thresholds assumed to be inhibiting natural or active regeneration of the study sites that will be used in this research are indicated on the diagram by numbers 8 to 11, and are as follows:

(8) Loss of seed source - The study sites are mostly surrounded by anthropic landscape with sparse or no native forest remnants. Deforestation caused the extinction of many plant species in the study areas' vicinities, which led to loss of seed source;

(9) Competition with exotic grass/herbs - The areas are dominated by an exotic grass sward and by herbs that compete with the remaining native plant species, thus inhibiting or even blocking the establishment of native species seeds and seedlings, if adequate management is not carried out;

(10) Herbivory and Diseases – Browsing and chewing of tree branches and seedlings by exotic vertebrates such as deer, sheep, goats, rabbits and hares are problematic for restoration practices in the study areas. These animals eat the seedling shoots and buds, thus affecting the plants' development when not killing them. The microhabitat formed by the rank grass may also create an ideal environment for fungal and/or bacterial development that may cause diseases to native seeds and seedlings, an extra threat to their establishment and survival;

(11) Altered soil properties – Deforestation, agriculture, pastoral practices and exotic species invasions do not solely affect the surface of the ecosystem, but the soil physical and chemical properties as well. Seeds and seedlings cannot establish themselves in the soil unless through assistance, such as active plantings. Even so, this does not necessarily imply that plantings will grow and survive on the site if soils are compacted, toxic, nutrient-poor, or the hydrological system has been altered in a way that water is too scarce for seedlings/seeds to absorb.

The main objectives of this research were to determine which threshold (or combination of thresholds) that is preventing woody tree species from establishing themselves and surviving on the study sites and how this can be reversed for the benefit of ecological restoration of New Zealand's dryland ecosystems.

1.2 General hypotheses

- Water availability is a limiting factor to the establishment of native woody species because of the current soil physical properties of the sites, which facilitate the colonization of the areas by exotic grass and weed species;
- The use of shelters will protect restoration plantings from weather elements, essentially direct solar radiation and high wind, and will decrease current elevated water evaporation levels, therefore making this fundamental resource more available to plants, and increase the probability of seedling survival and growth;
- Grass removal treatments may improve the chances of restoration projects by reducing the competition between native seedlings and exotic grasses and weeds for soil resources and for light;
- Native seedling establishment is hindered on the study sites because of the presence of domestic grazing animals and other types of herbivores, such as hare and rabbits. Therefore, restoration of the native vegetation will be more successful if seedlings are protected from predation through fencing.

2. Literature Review

2.1 Ecological Succession, Restoration Efforts, and Ecological Thresholds

Ecological succession is a natural phenomenon that every biological community undergoes to try to restore the natural balance between the biota and the physical environment, by either recovering or replacing the species that were lost, and reinstituting the ecological processes that may have ceased following a disturbance event (Johnson & Miyanishi, 2010). The timeframe between disturbance and recovery depends on the nature, duration, and intensity of the ecological impact (Hobbs & Norton, 1996). It is common in certain situations for 50 or 100 years to elapse before a satisfactory vegetation cover develops. In other situations, for example, on mining sites where there is extreme soil loss and mostly permanent soil damage, the original vegetation cover is most likely never to return (Bradshaw, 1997). A normal practice to assist natural succession on degraded sites is to sow or plant selected species to ensure recolonization of the area. Actively planting tree seedlings will readily provide soil organic matter, lower soil bulk density, bring mineral nutrients to the surface and accumulate them in an available form. This type of restoration effort involves choosing "nurse plants" (Gómez-Aparicio et al., 2004) that are easy to propagate, able to suppress weeds and grasses, and create suitable microclimate for seed survival and seedling establishment (Blakesley et al., 2002b; Widmann et al., 2005a). It is necessary to ensure the planting of matching or "framework" plant species to particular microsites that are able to endure the harsh conditions during the initial stages of the restoration process (e.g. compacted soils, soil salinity or toxicity, direct solar radiation, etc.) and will create a more suitable environment for later successional species to be re-introduced (e.g. increase soil organic matter and nutrient levels (Yates et al., 2000). Framework plant species are expected to repair the sink source or increase the potential for sinks to develop (Gênova et al., 2007) that will facilitate the return of lost species and ecological functions, and stimulate the successional process on their own (Cabin et al., 2002). As well as ameliorating soil physical and chemical properties and restoring the water cycle (Tang et al., 2009), assisted development of a vegetative cover has proven to be a fundamental step towards facilitating forest succession by providing perching opportunity for birds (Reay & Norton, 1999). Ecological regeneration may become self-sustaining in the long run with the return of pollinators and seed dispersers (Treca & Tamba, 1997; Reay & Norton, 1999).

Fire has also been used as a management tool for restoration of degraded cerrado vegetation areas in Central Brazil by reducing the density of the invasive African grass *Brachiaria* sp on the landscape with herbicide application, introduction of grazing animals (mostly cattle), and controlled fire (Marimon & Lima, 2001). By lowering grass density, the combustible material is reduced, thus lowering fire frequencies on grass-dominated ecosystems (Brooks et al., 2004; Ammondt & Litton, 2012). The use of fire or grazing animals as a restoration management tool is common in ecosystems that have co-evolved with fires and herbivory (Eiten, 1972; Walker, 1987) or present plant species with reproductive structures that can only germinate after a burning event (Eiten, 1972). However, these techniques must be used with care because burning of watersheds supporting certain types of vegetation may, on the contrary, increase erosion rates and degradation (Binkley & Fisher, 2013), and the constant tramping of grazing animals such as cattle can cause soil compaction (Yates et al., 2000) and their excrement can pollute the soil and waterways (Bilotta et al., 2007). Also frequent burning has been reported to reduce above and belowground biomass (Van Langevelde et al., 2003), facilitate biological invasions of more fire-resistant plant species (D'Antonio & Vitousek, 1992), and to benefit grass cover over shrub and tree species (Watkinson & Powell, 1997). In grassland areas in West Africa, restoration of former pasturelands proved more successful with fencing and consequently reduced grazing pressure (Mengistu et al., 2005; Hejcmanová et al., 2009; Campbell, 2010).

The restoration management tools discussed above involve techniques that basically try to stimulate natural regeneration by reducing stressors and introducing native plant species. However, the recovery of an ecosystem also depends on system components and processes that were probably altered after the disturbance (Brown & Lugo, 1994), as well as the system's resilience (Lugo, 1988). Resilience is the capacity of a system to absorb disturbance and reorganize while undergoing change so as to retain essentially the same function, structure, identity, and feedbacks (Folke et al., 2004; Walker et al., 2004). Resilience relies on biotic and abiotic interactions inside an ecosystem (Walker et al., 2009b). Whenever a disturbance breaks these interactions, the entire ecosystem can be affected because of changes in the ecological processes. If the changes are permanent (e.g. increase in soil salinity caused by irrigation) the original vegetation may not be able to re-colonize the site even after the stressors have been removed (e.g. cessation of farming and irrigation) due to the site no longer possessing the

necessary pre-disturbance conditions for that species to exist and persist. Currently, the manipulation of a site's environmental conditions, along with removal of stressors, to accommodate the native vegetation's requirements to survive in the area (Lugo, 1988) has become an appropriate tactic used by restorationists (Walker et al., 2009a). More and more, researchers have been looking into incorporating alternative trajectories of succession dictated by ecological thresholds and stochasticity (Pyke & Knick, 2005; Ammondt & Litton, 2012) that integrate a more holistic approach to restoration of degraded ecosystems that involves not only direct seeding or planting of seedlings, but also soil property amendment (Tang et al., 2009) and reintroduction of fauna (Carter & Newbery, 2004; Costa & DeLotelle, 2006). Moreover, the history and characteristics of the perturbation should integrate the state-and-transition model for ecological succession and restoration (Walker et al., 2009a).

The state-and-transition models in restoration ecology are based on the modern understanding that succession is a complex system in a dynamic-equilibrium state (Lewontin, 1969), instead of the gradual and linear change in species composition sequence suggested by Clements (1916), and that ecosystem regeneration follows different types of dynamics that are determined by environmental feedbacks that, in their turn, will dictate the trajectory of the ecological rearrangement in progress (Suding & Hobbs, 2009). The state-and-transition models describe the processes of perturbations that cause transitions between states and try to explain the relationship among degradation, community structure and ecological thresholds (Briske et al., 2003; Suding & Hobbs, 2009). Moreover, these models help determine whether the ecosystem will move on towards the original state, or form a novel ecosystem (Hobbs et al., 2006), with alternative or hybrid ecosystems along the way (Hobbs et al., 2009).

2.1.1 Ecological Thresholds

Any natural or anthropic interference in a biological community can provoke cascading effects on all ecological processes and make the ecosystem more susceptible to further degradation, such as invasion by exotic species (D'Antonio & Meyerson, 2002), species turnover (Jeltsch et al., 2011), local extinction of native species (Schleuning et al., 2009), changes in fire frequency and intensity (D'Antonio & Vitousek, 1992), soil erosion, and desertification (Zhao et al., 2005). The degraded state of an ecological community persists when either abiotic or biotic environmental

factors, henceforth called “ecological thresholds”, control the current ecological processes and prevent the return, or recovery, of the original biota (Allen et al., 2006). Ecological thresholds may be considered as ecological boundaries that determine the characteristics of an ecosystem according to environmental components and the interaction between them (Mark & McLennan, 2005). When disturbances somehow modify these components, the ecological “boundaries” can be considered as trespassed or crossed-over, and restorative processes will likely be stalled (Hobbs & Harris, 2001). If the system is severely degraded, where soil food webs and processes have been altered and the system’s resilience is impaired, the ecosystem forms an alternative stable state (Gunderson, 2000) because of “the extinction of ecological interactions” (Janzen 1974). It is complicated for the ecosystem to return to its historical or reference condition unless the ecological thresholds are somehow manipulated in order to reinstate some of the original environmental conditions (Heneghan et al., 2008) and the native vegetation can colonize the area again.

In New Zealand, an example of biological threshold is the effect of the extinction of many indigenous birds due to predation on community structure and composition of native forests and grasslands, which could not be reversed even after predators were removed (Saunders & Norton, 2001). Invasive species can drastically alter native ecosystems, especially on oceanic islands (Vitousek et al., 1997). Another example of biological thresholds is the presence of exotic grasses that often possess ecophysiological traits that can inhibit natural regeneration (Thaxton et al., 2010), change competitive dynamics of native plant communities (Bryson & Carter, 2009), alter the structure of food webs (e.g. “trophic cascades”; Polis et al., 2000), and change disturbance regimes (D'Antonio & Vitousek, 1992; Ammondt & Litton, 2012). Dense stands of nonnative invasive grasses prevent establishment or cause slow growth of native species in degraded grasslands in Panama (Hooper et al., 2002) and in Brazil (Hoffmann & Haridasan, 2008). Invasive grasses are numerous and highly competitive for light, water and nutrients and also hinder natural succession and restoration of dryland forests in Hawaii (Litton et al., 2006; Cordell & Sandquist, 2008). Fire frequency and intensity in northern tropical savannas in Australia have increased eightfold due to the presence of nonnative grasses (Rossiter et al., 2003).

Abiotic thresholds involve barriers to restoration and natural succession due to changes in microclimate (Pavliscak et al., 2015), soil physical and chemical properties, or water cycle (Trotter et al., 2005). Depending on the nature, intensity, and duration of the disturbance, changes to the abiotic characteristics of an ecological community may modify its entire structure permanently (Hobbs & Norton, 1996). Soil compaction is a common consequence of inadequate farming practices and long-term grazing (Yates et al., 2000). It unavoidably impacts soil-water availability to plants and affects one of the most important soil properties to vegetation development and distribution on a site (Proffitt et al., 1993). Plants are unlikely to develop any significant root growth in soil water levels near the wilting point (Nawaz et al., 2013). Besides, stem growth would also be exceedingly slow even during summer, when warmer temperatures would otherwise be favorable for plant growth, if soil water levels are below the ideal (Lambers et al., 2008). Intensive farming and grazing also affect the chemical properties of the soil (Liu et al., 2006). It is the combination of mammalian grazing and fertilizer application that consolidates the presence of non-native woody and herbaceous N-fixers across the grasslands in New Zealand, where herbivore-resistant and nutrient-rich plant species thrive in soils that suffered alterations in their natural nutrient levels through fertilizer inputs (Walker et al., 2005).

Efforts to restore local vegetation by tackling biological thresholds alone (e.g., planting seedlings, or removing predators) might be unfruitful if environmental conditions no longer support the reintroduction (or recolonization) of the original biota (Walker et al., 2003b). Significantly degraded sites normally require active restoration efforts that deal with both biotic and abiotic thresholds. However, unfavorable physical conditions of the environment need to be carefully analyzed and improved as they directly affect the structure of the communities by controlling species assembling (Johnson & Miyanishi, 2008) and, consequently, influence any restorative plan that involves manipulation of biological thresholds. Therefore, significantly degraded sites generally require active consideration of soil amelioration (Heneghan et al., 2008) and improvements to the microclimate in order to reverse some abiotic thresholds and assist regeneration (Nepstad et al., 2004).

2.2 Restoration of New Zealand's Dryland Zone

New Zealand's dryland zone is the eastern interior region of both islands which are drier than the coastal zone. The definition is based on water availability (average annual water deficit and average month water balance ratio) as a boundary limit. The indigenous dryland zone is covered by grasslands dominated by species with tussock or bunch grass habitat (Rogers et al., 2005). The two main types of tussock associations (Figure 2-1) are floristically diverse and used to be found from near sea-level to the alpine zone (Godley, 1975). The tall-tussock grassland, found in higher and wetter altitudes above the forest line, or above short-tussock grassland, in drier areas of the North and South Islands, is dominated by one or another of the larger species of snow-grass (*Chionochloa*), whereas the short-tussock grassland, usually dominated by species of *Festuca* and *Poa*, is mainly found in the drier and lower altitude parts of the South Island (Godley, 1975). The dryland zone is one of the most altered native ecosystems in New Zealand with only 30% of its original native vegetation area left (Walker et al., 2009a). The dryland zone has been greatly modified since humans first settled. The previous vegetation cover (before human arrival in about 750 BP) used to be dominated by trees and shrubs, and fire was periodic, normally within a 1,000-1,500 year cycle (McGlone et al., 2001). Currently, the native vegetation found in this zone (seral grassland and shrublands) is a result of fires and grazing used by settlers for agriculture and pastoralism. This indigenous community is in fact anthropogenic in origin (McGlone, 2001; Rogers et al., 2005), though it is regarded as the "de facto" natural vegetation cover (McGlone et al., 2001) and of conservation concern by New Zealand's Department of Conservation – DOC. Yet, little of this land area is formally under protection (only 1.9% is legally protected, Walker et al,. 2009); therefore, many of its indigenous plants and animals have become threatened or are at risk of extinction (Rogers et al., 2005).

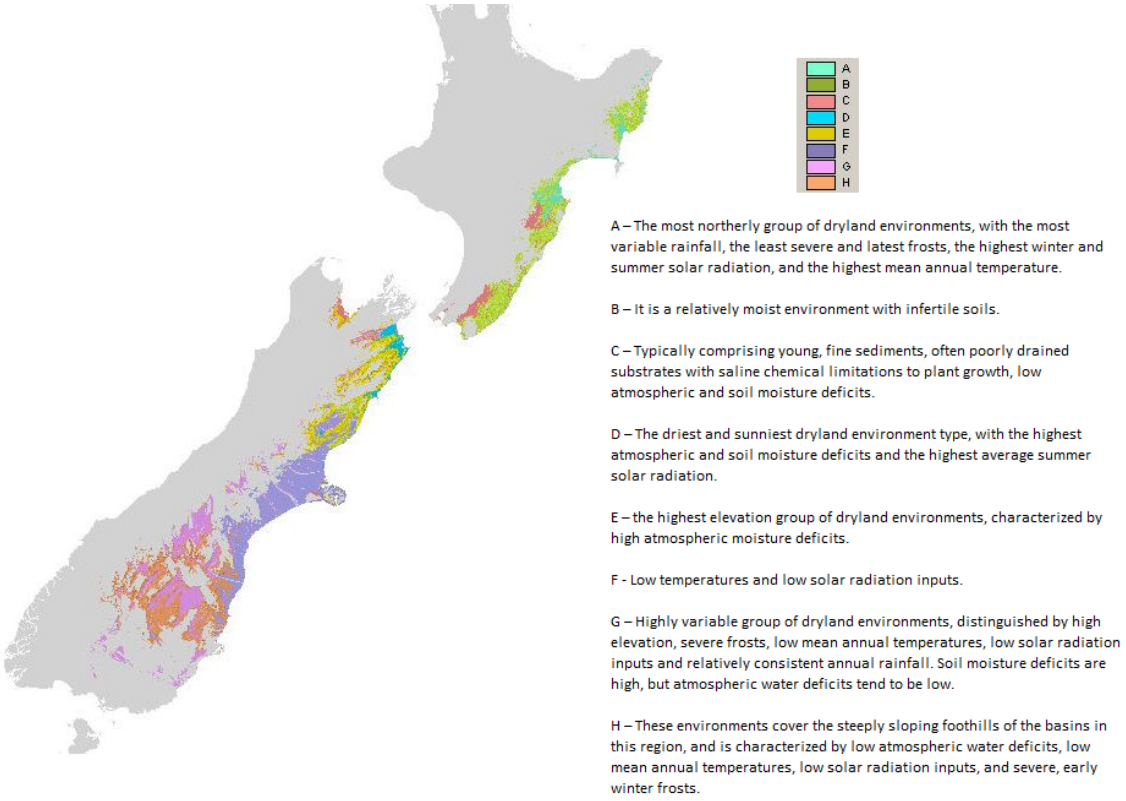


Figure 2-1 Dryland zone distribution in New Zealand (Rogers et al., 2005).

In the last *c.*150 years, grasslands and shrublands in the eastern part of New Zealand's South Island dryland zone have been perpetuated and succession onto the woody vegetation cover recognized to have existed in pre-human times has been retarded by a combination of fire, pastoral use and grazing by feral mammals (Worthy & Holdaway, 2002). Major environmental problems were already being reported by mid-1950s that were affecting land productivity throughout the grasslands and causing the destruction of native grass and shrub ecosystems, largely prompted by introduced plants and mammals (McWethy et al., 2009). Declining land and stock productivity as a consequence of the serious environmental degradation after decades of burning, grazing and the presence of exotic species (Brooking et al., 2002) triggered a change of tenure of many pastoral and/or agricultural lands that were later placed within the public conservation estate and managed by the Department of Conservation (Mark et al., 2009). Subsequently, some of these abandoned farmlands were aggregated into the conservation network, managed by government and non-government groups, to function as restoration sites

for the threatened dryland ecosystem (Standish et al., 2009). What was once regarded as insufficiently pristine for ecological conservation is currently viewed to be important for restoration of degraded ecosystems after conservationists started noticing that native plants were recolonizing some of these abandoned farmlands (see reviewed articles by Queiroz et al., 2014).

2.2.1 Ecological Thresholds Preventing Restoration of the Dryland Zones

However, transitions from exotic grassland to native woody communities do not always occur without human intervention (Hobbs & Harris, 2001). Many of these lands that were once covered by dryland woody vegetation have gone through degradation processes for decades that have transformed their original environmental characteristics to the point that ecological thresholds are now constraints to the re-establishment of the original plant species (Hobbs & Norton, 1996; Holl et al., 2000; Hobbs & Harris, 2001; Standish et al., 2007; Hobbs et al., 2009; Standish et al., 2009). Many environmental factors have been raised by Rogers et al. (2005) that are considered as impediments to the ecological conservation and restoration of dryland ecosystems in New Zealand. Although being of great conservation concern and threat, the dryland zone in the South Island is still continuously burned and overgrazed. Additionally, areas that could be used to help restore the vegetation, such as abandoned farmlands, are now colonized by a rank growth of exotic grasses (e.g., *Agrostis capillaris*, *Anthoxanthum odoratum* and *Holcus lanatus*) and herbs (*Hieracium* spp.) (Rogers et al., 2005; Walker et al., 2009a).

Restoration efforts on previously farmed areas in the eastern New Zealand dryland zone are extremely difficult because these areas are prone to biological invasions due to the altered soil physical and chemical conditions (Jesson et al., 2000; Walker et al., 2003b; Walker et al., 2005). Although some pasture species are lost after abandonment, the more aggressive and competitive ones dominate and outcompete native plant species (McQueen et al., 2006), eventually replacing them. Native woody vegetation recovery is also hindered by herbivory and fire, that have contributed to a regime shift of former native grasses and shrubs to one dominated by invasive plant species (Walker et al., 2009b). Fire frequency is common in dryland areas, especially during dry summers, and has a long history in this ecosystem, associated mainly with volcanic eruptions and lightning strikes (McWethy et al., 2009). However, fire events have never been sufficiently frequent or widespread in a dissected landscape to result in strong selection for fire-

adapted traits in the flora (McGlone et al., 2001). Serotiny is limited to populations of the *Myrtaceous* shrub *Leptospermum* and is extremely low (Harris, 2002), and most native woody and herbaceous species are fire-sensitive (Bond et al., 2004). During the pre-European era there was a low diversity of non-native plants available to exploit the reduction of forest. European burning, however, enhanced the spread of an imported pool of fire-adapted non-natives with serotinous or heavily protected capsules (e.g., Hakea) and/or large seed banks (e.g., *Ulex europaeus, Calluna vulgaris*), and enhanced the opportunity for the expansion of numerous ruderal non-native species across the grasslands (Craine et al., 2006). The presence of exotic fire-prone species, such as gorse and pine trees that form a thick litter layer, increased dryland's natural susceptibility to fire and, combined with extensive farming practices, intensified the naturally low soil-water content (McGlone, 2006). Low soil-water content is a natural characteristic of arid and semi-arid ecosystems related to soil and climatic conditions (Yuan et al., 2009), and already submits the vegetation to soil water deficit during the dry summer and drought spells, causing vegetation dieback (Tyree, 2003). In disturbed areas where there is a dense grass sward, soil-water deficit escalates because of the root mat of the grasses that can quickly absorb any water content that reaches the soil (Clary et al., 2004). Low annual precipitation in temperate grasslands makes the vegetation vulnerable to frost during the cold seasons (Körner, 1998; Inouye, 2000). Winter frost can intensify the negative effects of low soil moisture and cause mortality of native seeds and seedling, and be even more damaging to restoration plantings due to exposure, as opposed to seedlings growing under a denser forested area (Bannister, 2003).

Restoration efforts on abandoned farmlands are also constrained by the human induced nutrient enrichment of soil. Native grasslands and trees in New Zealand occupied cold or wet, low-nutrient-supply ecosystems and few of the plant species were well suited for growth with high nutrient supply. Nitrogen-fixing plants, which are dependent on high phosphorus levels, are uncommon in the native flora, and the few species that have this trait are slow-growing and far less competitive on the nutrient-rich soils associated with agricultural development (Craine & Lee, 2003). Consequently, exotic species now predominate over native plants on formerly pastoral and agricultural lands in New Zealand (McAlpine et al., 2009). Furthermore, New Zealand plant species did not evolve in the presence of herbivores; hence, they are not resilient

enough to overcome predation. Herbivory can curb native forest regeneration when seeds, seedlings and adult plants are grazed at a faster rate than the plants can establish on the site (Towns et al., 1997; Atkinson, 2006). Predation on native pollinators and seed dispersers exacerbates seed limitation (Clout & Hay, 1989) and restrains forest regeneration in New Zealand even further. Therefore, native seedlings used in restoration plans in the dryland zone of New Zealand not only have to compete with invasive plants for resources, but also cope with the modified environmental conditions (Craine & Lee, 2003; Walker et al., 2009a) and survive predation by introduced mammals (Holland et al., 2002; King & Wilson, 2006).

2.3 Managing Ecological Thresholds for Restoration Purposes

Ecological succession spontaneously occurs in every ecosystem on a daily basis after certain natural phenomena (e.g., hurricane, typhoon, etc.) cause disturbances in the biological community. Secondary succession, on the other hand, is the term given to vegetation recovery on disturbed areas that were once vegetated but were converted to agricultural lands at some point, and then abandoned (Finegan, 1984). This phenomenon has been the focus of many researches for decades and in different terrestrial ecosystems to try to understand how succession happens and the stages involved, so that the knowledge acquired could be applied to induce successional processes in areas where forest regeneration does not take place spontaneously (Horn, 1974; Aweto, 1981; Guariguata & Ostertag, 2001; Rovai et al., 2012). In doing so, restorationists have realized that it is crucial to integrate in the restoration plan the ecological factors or thresholds that were breached by the disturbance and are limiting secondary succession. Therefore, restoration plans must include the management of anthropogenic niches to decrease the impact of invaders and other ecological elements by actively seeding or planting native seedlings, controlling/removing exotic species, and managing abiotic elements (e.g. soil compaction, water deficit, or lack of tree canopy). Additionally, it is important to know the historic or past land use practices in the area to have a more thorough understanding of the effects these practices might have had on the site's current environmental conditions.

2.4 Plant-Soil-Water Relations, Plant Physiology and Implications for Restoration

The structure and nature of soils are of relevant importance to vegetation communities (Passioura, 1991). Soils, collectively with other environmental factors, such as climate and water availability, determine the type of vegetation that is formed on a particular landscape. The organization and structure of vegetation communities vary according to the chemical and physical properties of the soil, and any environmental disturbance (e.g. deforestation, plowing, or draining) directly impacts soil properties; consequently, affecting both plant growth and community composition (Burke et al., 1998; Kozlowski, 1999).

2.4.1 The Relationship between Soil Physical Properties and Plant Establishment

Soil physical properties are directly linked to the growth and distribution of trees. Along with climate, soil physical properties influence the development of plants; hence, the formation and maintenance of an ecosystem through their effects on soil moisture regimes, aeration, temperature profiles, soil chemistry, and the accumulation of organic matter (Kramer, 1995). It is important for any ecosystem management to understand in what way soil particles respond to environmental changes (engineering behavior) and how they are directly correlated to soil texture, structure, porosity, and depth (Binkley & Fisher, 2013). The texture of a soil is its "appearance" or "feel", and it depends on the relative sizes and shapes of the particles as well as the range or distribution of those sizes (Dexter, 2004). The soil mechanics behaves according to soil texture and grain size that is most abundant in the soil profile. Mineral soils are usually grouped into three broad textural classes – sands, silts, and clays – and the most important differences in soil texture relate to the surface area of particles of different sizes (m^2/g). Particle size will determine soil texture with important effects on the soil's water-holding capacity, aeration, organic matter retention, and vegetation growth (Rendig & Taylor, 1989).

Soil texture determines soil structure, which basically depends on the size of the particles, how they aggregate and form pore space (capillary space) within the soil horizon. Capillarity pore spaces affect soil aeration, hence water movement through the soil profile and water availability to plants (Kramer, 1995). Soil water-holding capacity, or the amount of water retained in a soil after rain or irrigation, is also directly affected by the presence of vegetation and soil management of agricultural activities (Zhang et al., 2001). Infiltration rates in forest soils are

greater than in agricultural or pastoral soils with similar physical structure because a heterogeneous vegetation cover (as opposed to monocultures) adds more soil organic matter and promotes plentiful soil flora and fauna activity that influences pore volume (Ferrez et al., 2011). Deforestation, followed by cultivation and pastoral activities, disturbs a soil's natural proportion of capillary pore spaces and increases its bulk density (Chiu et al., 2012). Soils with high bulk density (or compacted soils) have lower soil-water holding capacity and offer more resistance to root penetration. They become less adequate for tree growth and present reduced aerobic microbe and root activities, and may also develop puddled areas and stimulate anaerobic conditions (Binkley & Fisher, 2013). On former agricultural lands, the addition of organic matter into the soil or any other technique that can reduce soil bulk density, improve infiltration and prevent puddling (Abdollahi et al., 2014) can be determinative for seedling establishment and favorable ecological restoration (Romic et al., 2008).

2.4.2 Soil Physical Characteristics and Soil Temperature

Soil temperature, similarly to air temperature, has a diurnal as well as a seasonal variation pattern, and fluctuates in correspondence to climate and other variables, but it is often warmer during the day and in the summer, and drops more quickly during the night or during the cold seasons (Kramer, 1995). The importance of soil and air temperatures for plants is that these factors are also responsible for evapotranspiration rates and soil-water movement; consequently, they influence the amount of water that is available to plants (Lockart et al., 2013). The presence of roots in the soil causes a rapid decrease in soil water around the roots and the soil may become depleted of this resource during warm days when the amount of water absorbed by transpiring plants exceeds the amount of water that infiltrates the soil (MacFall et al., 1990). As temperatures cool down in the evening, this water-depleted root zone can be rewetted, and the speed at which this takes place depends on the soil's hydraulic conductance (Kramer, 1995).

Water movement through the soil depends on evaporation rates from the surface of the soil and absorption by the roots of transpiring plants. Capillary rise (or upward movement of water in the soil) also depends on soil texture (Saxton & Rawls, 2006), which tends to be more rapid in fine-textured soils than in coarse-textured soils (Kramer, 1995). Vegetation cover influences soil-water movement by controlling evaporation rates. Under well-developed canopies of forested

areas, the soil surface is protected from direct solar radiation and from winds by the organic layer, which has low thermal conductivity and moderates soil temperature fluctuations (Hu et al., 2013). In the absence of forest canopy, topsoil temperature may be much higher than air temperature because of the absence or reduced organic layer cover (Fisher and Binkley, 2013). In cold climates, extremely low temperatures can cause frost to accumulate on the surface of the soil. Forested areas buffer the soil from freezing temperatures, whilst in bare soils, freezing generally occurs earlier and penetrates in deeper horizons (Dulamsuren & Hauck, 2008). Even the existence of few trees in an area can reduce extreme temperatures in the soil and plant mortality by blocking cold or hot air currents higher above the ground (Binkley & Fisher, 2013).

2.4.3 Soil Physical Properties and Soil Moisture Content

The formation and distribution of vegetation around the world is related to climate patterns and soil moisture. Soil type dictates soil water-holding capacity and, along with precipitation rates and other climatic factors, largely influences soil moisture and the availability of water to plants (Farmer et al., 2003). Soil moisture is also important for soil microbes, and has a great influence on soil temperature and aeration (Binkley & Fisher, 2013). The availability of soil water to plants depends on its potential and on the hydraulic conductivity of the soil (Kramer, 1995; Lockart et al., 2013). As water drains from the soil, macropores empty and water is present only in capillary pores, which hold water together with strong negative potential and also retard the flow of water (Horn & Smucker, 2005). Infiltration and water retention depend on soil texture. Fine-textured soils - clay and silt - have a higher retention capacity for water than sands, and can store larger amounts of water. However, fine-textured soils can lose their structure more easily than sandy soils, and become compacted after mechanization (Horn et al., 1995). Any activity that modifies vegetation cover and disturbs soil structure will have an influence on soil moisture and, consequently, on the soil's capacity to support vegetation (Saxton & Rawls, 2006). Soil depth (rooting depth) and stoniness are other factors that influence soil moisture and the amount of water that can be absorbed by plants (Webb et al., 1993b). Plants growing in shallow or stony soils usually have poor overall plant development due to physical and hydraulic restrictions common to this type of soils (Kramer, 1995).

Excess water can also be harmful to plants. Hypoxia/anoxia condition is detrimental for most species of higher plants and their development (Drew, 1997). Hypoxia is common in compacted soils (Pfeifer et al., 2014) and where the upper surface of the zone of saturation (water table) is very close to the root zone of the plants (Vartapetian & Jackson, 1997). The height of the water table fluctuates between wet and dry periods, and a reasonably high water table is not necessarily detrimental to plant growth as long as there is little fluctuation in its level (Binkley & Fisher, 2013). Root anoxia will happen when the oxygen content of air in soils falls much below the 20% found in the atmosphere, and in compacted soils, the concentration of carbon dioxide may rise in extremely wet soils to 5% or 6% and oxygen levels may drop to 1 or 2% by volume; thus considerably affecting plant survival (Good & Paetkau, 1992).

2.5 Environmental Stressors and Plant Physiology

Though ecological restoration is regarded as an important tool to repair environmental damages caused by anthropogenic activities (Dobson et al., 1997; Hobbs & Harris, 2001), the recovery of the historic ecological state can be extremely difficult because of the loss of fundamental abiotic and/or biotic factors (Rogers et al., 2005) that were vital for the existence of the original biota. In the previous pages, it was stated the relevance for restoration plans of having a comprehensive knowledge of the causes of degradation and how particular environmental characteristics of the present degraded condition are preventing the recovery of native vegetation on a site. Plant survivorship, growth, as well as morphology (e.g. leaf size) and productivity are directly linked to the environmental conditions in which the organism is growing (Poorter et al., 2012) and such data have long been used as an assessment of the success of restoration projects (Ruiz & Aide, 2005). Certain visual plant responses to environmental stressors, such as leaf necrosis, wilting and shedding of leaves, can definitely provide an assured indication that plants are not in a favorable environment. However, plants in these circumstances usually do not recover even after some kind of site improvement is applied (Pallardy, 2008) and restoration efforts are compromised.

Knowledge of plant physiological responses to environmental stress can be of great advantage for restorationists, because they are readily detectable by adequate equipment before any visual symptoms are observable (Kooten & Snel, 1990). Therefore, physiological tools can yield data

at a temporal scale that enables decision making to occur during projects. They also enable restorationists to reevaluate the progress of the project and make changes, modify environmental conditions to help plants acclimatize and avoid or minimize drawbacks (Cooke & Suski, 2008). All the same, physiological parameters of individuals have received little attention in the context of restoration, despite the fact that understanding how a system works (i.e., how biotic and abiotic elements interact) is a prerequisite to effective conservation (MacMahon & Holl, 2001).

Physiology is the key response mechanism linking both organism and population to their environment (the concept of "physiology/life-history nexus" in (Ricklefs & Wikelsk, 2002). Physiology can drive and constrain organismal responses to environmental pressures, such as those originated from disturbances and degradation, which ultimately structure ecosystems and regulate the organism's performance, environmental tolerances and capacity to acclimatize to new ecological conditions (Spicer & Gaston, 2009). Physiology is responsible for the fitness of an organism (Feder et al., 2000) and depends on both heritable and epistatic genetic variation (Travis et al., 1999). Physiological responses of terrestrial organisms are largely affected by biotic and abiotic features, such as light levels, water availability, and herbivory (Nilsen & Orcutt, 1996; Nelson et al., 2003; Ehleringer & Sandquist, 2006), and early responses to stress can make a difference as to whether an organism survives or perishes (Bohnert & Sheveleva, 1998). In plants, environmental stress triggers physiological responses that can be detected at the leaf level, though the stimuli could have taken place in the leaf itself or in any other part of the plant. As a consequence, all plant parts are integrated in defending the organism from the stressor by producing hormones and enzymes that will regulate carbon assimilation and allocation of photoassimilates to different parts of the plant (Poorter, 1999), stop stem growth and leaf production (Givnish, 2002), and delay or advance the phenological cycle in order to survive under environmental stress and be able to resume activities in a more favorable period (Chaves et al., 2003).

Two physiological techniques were selected to measure the responses of the restoration plantings to the treatments implemented in this research: chlorophyll fluorescence (quantum yield or Y-values) and carbon isotope signature ($\delta^{13}C$). These physiological measurements can assess the level of stress on plants caused by water availability, intense solar radiation and high temperatures, for example. Therefore, it is expected that these physiological data will provide

some insights on how the native woody tree species were coping with the current environmental conditions of the sites and whether the type of ground and aboveground treatments caused some kind of environmental amendment that acted as facilitator for seedling establishment.

2.5.1 Environmental Factors as Stressors

Plants, when under a stress force, may have part or all of their performance decreased below an expected value (Kozlowski & Pallardy, 2002). Odum (1985) considered a stress to be "any syndrome that interrupts, restricts or accelerates the normal processes of a plant or its parts". Different environmental factors can become stressors to an individual plant and affect its development (henceforth called "stressed"). Environmental stressors affect the plant's development by impacting photosynthesis either by forcing plants to regulate stomatal conductance or mesophyll photosynthetic capacity (Kozlowski & Pallardy, 1997). These are called "short term" reactions to environmental conditions, and once the environmental conditions improve, the plants are able to restore their photosynthetic capacity (Zhou et al., 2014). If stressors are frequent and of long duration, however, long-term morphological changes, such as reduced stem growth, can occur (Poorter, 1999).

Water availability

Water availability directly influences photosynthesis. Low water supply reduces photosynthetic rates by closing stomata, decreasing the efficiency of carbon fixation process, suppressing leaf formation and expansion, and inducing leaf shedding (Ort et al., 1994; Chaves et al., 2002). Leaves of trees growing in dry soil may not develop severe water deficits if the relative air humidity is high. Conversely, when relative humidity is low, even though soil-water supply is high, leaves still tend to dehydrate (Kozlowski & Pallardy, 1997). Leaf water deficits depend on relative rates of absorption and transpiration, and not on absorption alone. Stomatal inhibition of photosynthesis of plants in dry soil is not entirely traceable to leaf dehydration, but more closely related to soil-water status than to leaf water potential (Ψ), suggesting that stomatal closure is directly influenced by soil-water levels (Chaves et al., 2002; Golluscio & Oesterheld, 2007). The stomata of plants may close before the leaf loses its turgor completely due to the ability of roots to "sense" soil-water deficits. Plants in dry environments, consequently, tend to present a more

conservative water use attribute and the capacity to down-regulate its photosynthetic capacity and maintain water-leaf and CO_2 status (Morison, 1996; Ferrio et al., 2012) and avoid dehydration. Xeric plant species can normally maintain photosynthesis at quite negative leaf water potentials (Ψ), as soil-water levels decrease, compared to more mesic plants (Kozlowski & Pallardy, 1997).

Photosynthetic capacity reduces as an effect of increased resistance of CO_2 diffusion to the chloroplasts. Temporary midday reductions in photosynthesis occur regularly and have often been associated with stomatal closure, which limits CO_2 absorption by leaves. Effects of prolonged drought on plants, however, may cause failure of stomata to reopen fully and injuries to the photosynthetic apparatus (Lambers et al., 2008), along with morphological consequences of such situation (Caldwell et al., 1998). Drought is one of the most important factors that limit growth of plants in any environment (Kozlowski & Pallardy, 1997; Tyree, 2003), by having a direct effect on plants' physiological and morphological development (Atkin et al., 2006; Cernusak et al., 2007; Boyden et al., 2008; Coopman et al., 2010; Cieraad et al., 2015). On the other extreme, excess humidity also has negative impacts on a plant's physiological responses (Schlüter & Crawford, 2001). In plants in anaerobic conditions, the leaves possess higher metabolic activities in addition to photosynthetic carbon fixation, and species can either sustain shoot elongation during anoxia, or survive the unfavorable lack of O_2 but without having any shoot growth (Barclay & Crawford, 1982). Excess water reduces CO_2 absorption by leaves and may cause injuries to the photosynthetic apparatus and mechanism. In prolonged flooded conditions, photosynthetic capacity is drastically reduced and leads to halting of leaf and stem elongation, leaf injury and abscission and root atrophy and deterioration (Kozlowski, 2012).

Light

Solar radiation is fundamental for photosynthesis; therefore, light levels will induce or suppress stomatal opening and, consequently, regulate photosynthesis according to irradiance (Hanba et al., 2002). Photosynthesis normally suffers a reduction when plants are in shaded conditions (Farquhar et al., 1989b). On the other hand, when plants are exposed to extreme light for long periods of time, induction happens (Adir et al., 2003). This phenomenon occurs when light intensity increases and photosynthesis reaches a compensation point at which gas exchange

between the leaves and the atmosphere is cancelled out due to the equal balance between photosynthetic CO_2 uptake and its release in respiration (Ort, 2001). The light compensation point varies with plant species, genotype, leaf type, leaf age, CO_2 concentration of the air and temperature, and type of environment (Pacala et al., 1996; Poorter, 1999). As light levels increase, so do temperatures, and plant respiration has to increase faster than photosynthesis to compensate for the elevated CO_2 consumption by the plant cells (Chaves et al., 2002). The rate of photosynthesis eventually becomes relatively constant when light saturation occurs. Plants regulate their photosynthetic machinery as a photoprotection mechanism for when irradiances are high and water availability is low (Chaves et al., 2002). It has even been reported that, under intense irradiance levels, plants down-regulate photosynthesis and biomass productivity more than necessary (Ort, 2001) to maintain water status in leaves and protect the plant from photodamage (Catoni & Gratani, 2014). This physiological reaction to high light, on the other hand, can eventually affect the plant's growth (Adams III et al., 2013).

Temperature Effects

Rising air temperature normally increases net photosynthesis up to a point where, if temperature continues to increase, it starts declining quickly. For most temperate-zone plant species, photosynthesis rate increases from near freezing temperatures to an optimum level between 15°C and 25°C (Kozlowski et al., 1997). Most New Zealand native plants have low tolerance to temperature extremes (Wardle, 2002), with the high temperature optimum of 27°C for assimilation and growth having been observed in kauri and various podocarps (Hawkins & Sweet, 1989). Air temperatures do not affect photosynthesis alone, but interactively with light intensity, soil temperature, water availability and preconditioning effects of environmental factors (Pacala et al., 1996; Poorter, 1999; Chaves et al., 2002). Extreme temperatures can cause tissue damage, affecting metabolic processes, and reducing photosynthesis (Kratsch & Wise, 2000); hence, leading to reduction in biomass production and plant growth (Yang et al., 2005). Long-term extreme temperatures may have serious effects on plant functioning because photosynthesis tends to continue increasing, while respiration begins to decrease, when temperatures are outside the normal range for the plant species. When temperatures are high,

photosynthesis is reduced because of stomatal closure as a consequence of increased water vapor inside leaf cells (Kozlowski & Pallardy, 1997).

Damages to plant tissue and photosynthesis regulation can also take place when temperatures are drastically reduced (Fitter & Hay, 2012). Fast reductions in temperature usually cause severe damage to plant death (Karpinski et al., 2002). Many sub-tropical plants grow poorly or become damaged at temperatures between 10°C and 20°C. For many common canopy tree species in New Zealand, optimum temperature ranges for efficient photosynthetic rates are higher than the common range for temperate plant species (between 15°C and 25°C), which makes many indigenous tree species more sensitive to low or near-freezing temperatures (Hawkins & Sweet, 1989; McGlone et al., 2001). Frost damage only occurs below 0°C, and is associated with temperature effects on the photosynthetic machinery (Kozlowski & Pallardy, 1997). Low temperatures impact the biochemical steps of photosynthesis (electron transport and activity of the Calvin cycle) and lead to photoinhibition and photoxydation (Kozlowski & Pallardy, 2002). As a defense mechanism, the plant can reduce its photosynthetic capacity and the quantum yield of photosynthesis, as evidence of decline in chlorophyll fluorescence (Ort, 2001). Photosynthesis is affected by temperature change in the atmosphere as well as in the soil. Depending on how long the plant roots are under either low or high soil temperatures, CO_2 uptake is reduced due to stomatal closure and non-stomatal inhibition, leading to reduced photosynthetic efficiency and reductions in photosynthesis (Kozlowski & Pallardy, 1997).

2.6 Measuring of Stress – Chlorophyll Fluorescence Reading

Restoration projects stand higher chances of succeeding when they include in their planning as much information about the degradation process itself, the ecological thresholds and physiological plant responses to environmental changes (Cooke & Suski, 2008). A technique developed in the mid-1980s by (Bradbury & Baker, 1984) involved the biophysical interpretation of pulse-modulated fluorescence that could be performed on the site without destroying the plants and measure the level of stress of a plant through the trade-off between photosynthetic efficiency and photochemical reactions (Krause & Weis, 1991; Sánchez & Quiles, 2006). Under normal light conditions, fully functional leaves in healthy plants react similarly, with over half of the solar radiation being absorbed by photosystem II chlorophylls and

redirected by a process that operates within the antenna ensemble of photosystem II, which harmlessly discharges excess photon flux energy as heat (Niyogi, 1999; Horton & Ruban, 2005). This thermal dissipation process (non-photochemical quenching) of chlorophyll-excited states participates with fluorescence emission as well as with photosynthesis (Ort, 2001).

In the photosynthetic apparatus of plants, light is absorbed by the antenna pigments of the photosystems I and II, and a photon-excited chlorophyll molecule moves to a higher energy state (excited state). The excited chlorophyll is extremely unstable and there are four possible pathways for disposing of its energy (Krause & Weis, 1991). The chlorophyll fluorescence emission pathway is the only process that will be discussed in this thesis. In this pathway, the chlorophyll molecule returns to its ground state by emitting fluorescence, mostly through the photosystem II antenna (photosystem I only contributes around 1-2% of the total fluorescence). Hence, changes in this radiation reflect the state of photosystem II (Krause & Weis, 1991). The quantum yield of photosystem II is obtained as a ratio of the variable fluorescence emission (Fv) and maximum fluorescence yield (Fm). This ratio (Fv/Fm) is an important and easily measurable parameter of the physiological state of the photosynthetic apparatus in intact plant leaves (Baker, 2008). The values of Fv/Fm in unstressed plants adapted to dark are in the range of 750-850. Environmental factors, such as light, CO_2 concentration and temperature, as well as chemical compounds (including some herbicides) affect photosynthesis and photosystem II efficiency; consequently affecting these Fv/Fm values (Krause & Weis, 1991). Environmental stressors may force the plant's photosynthetic machinery to exceed its capacity and lead to photoinhibition, thus causing damage to the photosynthetic centers (principally photosystem II) (Sánchez & Quiles, 2006), inactivation of photosynthetic enzymes, damage to the membrane of chloroplasts and, consequently, to leaves (Taiz & Zeiger, 2010). Genty et al. (1989) introduced an expression to calculate quantum yield of photochemical energy conversion (see Equation 3-3 in Chlorophyll Fluorescence Measurement section), which has been used on fluorometers to obtain the yield parameter.

2.7 Measuring Stress in Plants through Carbon Isotope Analysis

Sustainable environmental policies require increasing knowledge of the direct effect of human activities on the environment and of the subsequent response of plants and natural systems

(O'Brien et al., 2006). Physiological studies, in this case, are a precise method to determine the ways in which plants react to different environmental conditions and can provide vital information on how to improve the current situation for the benefit of restoration projects (Cooke & Suski, 2008). The information obtained from physiological assays, however, is often limited by sample size because time or technical resources are limited (Lambers et al., 1998). Although these types of studies often provide accurate data on instantaneous plant water status, photosynthesis or transpiration rates, they are difficult to extrapolate over larger temporal and/or spatial scales (Ferrio et al., 2003). In this context, a time-integrated physiological indicator such as carbon isotope ratio ($\delta^{13}C$) of plant tissues, although based on more indirect assumptions, can reflect long-term plant responses to different environmental conditions and stresses (Vogel et al., 1993).

For over a century there has been interest in understanding the relationships between water consumption by plants and overall productivity (Cernusak et al., 2013). Ecologists have been interested in how leaves of different species varied in these parameters, especially in response to seasonal and geographical changes in moisture availability and how these responses influenced both structural and physiological features of natural vegetation (Ferrio et al., 2003). From these studies it became clear that there were substantial variation in the relationships between water consumption and biomass production. Plants could then be divided into two distinct groups on the basis of their water requirements for growth: C3 and C4 plants (Farquhar et al., 1989b). Today, field micrometeorological and physiological approaches are routinely combined in field investigations, and carbon isotope analysis has emerged as a means of spatially and temporally integrating carbon and water relations parameters (Barbour et al., 2007; Cernusak et al., 2013).

Water deficit is a common and widely spread experience for most plant communities (Jensen et al., 1998; Sperry & Hacke, 2002; Nicholls, 2004). Plants are able to adjust the rate of water loss by transpiration through regulation of stomatal aperture (Figure 2-2), which also affects the rate of CO_2 assimilation and, consequently, plant production and growth (Ort et al., 1994; Meziane & Shipley, 2001; Chaves et al., 2002; Padilla & Pugnaire, 2009). Plant transpiration efficiency (W), the ratio of dry matter produced to water used, is a crucial feature in determining productivity and probability of survival. Carbon isotope discrimination (δ) against ^{13}C is

negatively related to plant W in C3 plants (Ehleringer & Cooper, 1988). Transpiration or photosynthetic efficiency is dependent, in part, on the intercellular to atmospheric partial pressure of CO_2 ratio (p_i/p_a), which is strongly influenced by the environment, and indirectly on carbon isotopic discrimination (Farquhar et al., 1982). Experiments have shown linear negative relationships between carbon isotopic ratio measured in whole-plant dry matter and plant water-use efficiency in several plant species (for a review see Farquhar et al., 1989b). Consequently, it has been proposed that the analysis of carbon isotopic discrimination, or carbon isotope signature, may be used for assessing water-use efficiency in ecophysiological studies (Tognetti et al., 2000; Adiredjo et al., 2014; Scartazza et al., 2014).

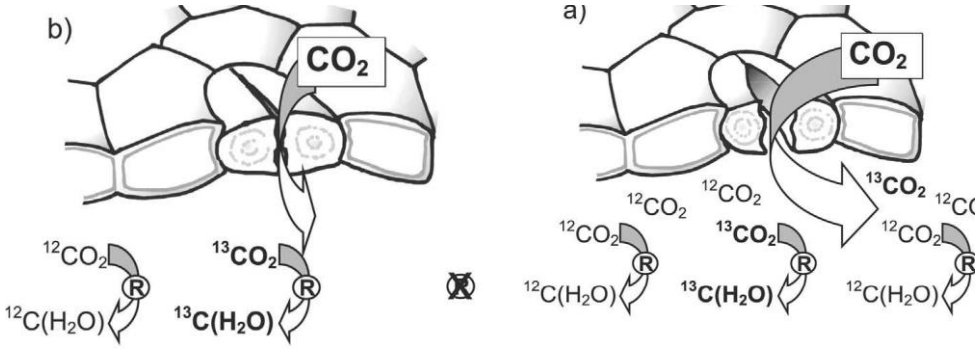


Figure 2-2 Simplified scheme of the relationship between carbon isotope composition ($\delta^{13}C$) and stomatal conductance: (a) high stomatal conductance, low discrimination; (b) low stomatal conductance, high discrimination (Ferrio et al., 2003).

Variability of Carbon Isotope Fractionation during Photosynthesis

Early surveys of the carbon isotope ratios of C3 and C4 plants fall into two non-overlapping categories. The C3 grass species all have δ-values between -22‰ and -34‰, while C4 species fall between -9‰ and -16‰. As atmospheric CO_2 has a value of about -7.5‰, the average fractionation in the C3 group is -19‰ compared with -5‰ for the C4 group. This difference in isotope composition is related to the distinct metabolic pathways (C3, C4 and CAM plants), and $^{13}C/^{12}C$ ratio is negative if the carbon sample contains less of the heavy isotope (^{13}C) than the standard (Vogel et al., 1993). While isotope ratios of the two groups of plants are related to function and structure, the variation within each category is due to the influence of

environmental factors on the kinetics of photosynthesis (Farquhar et al., 1989b). Isotope ratio measurements can thus be used for metabolic responses of plants to varying environmental factors, especially in C3 plants (Ferrio et al., 2003). Variation in $\delta^{13}C$ is caused by genetic and environmental factors that combine to influence gas exchange through morphological and functional plant responses to landscape, altitude, soil moisture, irradiance, temperature, nitrogen availability, salinity, and atmospheric CO_2 concentration (Diefendorf et al., 2010; Tezara et al., 2010; Cernusak et al., 2013).

3. Methods

3.1 Study Sites

3.1.1 Rank Grass Sites

The Rank Grass study sites comprise three trials: two in Northern Canterbury (Tiromoana Bush and The Willows Reserve) and one in the Mackenzie Basin (Dierickx Farm). All three areas were former farmland and are currently characterized by a rank growth of exotic pasture species, dominated by exotic grasses, clover and herbs, whose densities vary with soil-moisture levels. The study areas are within the range of the South Island's dryland zone, and present relatively similar climate patterns, as well as soil types (see Appendix:Soil Analyses), although the Dierickx Farm site is at higher elevation and colder climate (Figure 3-1).

Figure 3-1 Location of the North Canterbury sites: Tiromoana Bush and The Willows Reserve. Source: Esri, DeLorme, MapmyIndia, © OpenStreetMap contributors | Eagle, LINZ.

- *Tiromoana Bush*

The trial set up in Tiromoana Bush (-43.10° 172.85°, 400 ha) is located in a shallow valley at the foot of a *Pinus radiata* plantation forest, to the south, and another restoration planting to the northeast. The study site is at 141 m above sea level (a.s.l.) and approximately 2.1 km from Canterbury Regional Landfill area (Figure 3-2). The average annual rainfall in the Northern Canterbury region is around 600 mm, mainly in winter and spring, although averages can go as high as 919 mm (Henshaw, 2012). Typical summer daytime maximum air temperatures range from 18°C to 26°C, but may rise to more than 30°C. Coastal North Canterbury experiences cool northeasterly breezes, reducing temperatures in summer. Winters are cold and frosts occur frequently. Typical winter daytime maximum air temperatures range from 10°C to 14°C (Figure 3-11). The soil is typically moist, especially during winter, but extremely low soil moisture can also occur during the summer. Tiromoana Bush, also known as the Kate Valley Conservation Management Area, is being managed for the conservation and restoration of degraded lowland native shrubland and forest (Norton, 2012). The region where Tiromoana Bush is located is believed to have been covered by coastal broadleaved, mixed podocarp-broadleaved and black beech forests in pre-human times. Currently, the original native vegetation is confined to small remnants on surrounding hills, with some patches of gully and riparian shrubland and regenerating forest, as well as scattered shrubland on steep faces, tussocks on higher slopes and wetland species in riparian and seepage lands through Tiromoana Bush. The dominant vegetation type is pasture, though some indigenous forest cover remains mostly composed of *Kunzea ericoides*. Exotic shrubs such as gorse are also present, and the species and density of exotic grasses varies along the soil moisture gradient (Arihafa, 2008).

Restoration efforts in Tiromoana Bush are restricted due to the presence of exotic plant species within and in the surroundings of the conservation area boundaries. There are a number of exotic grasses and forbs in the area: cocksfoot (*Dactylis glomerata*), Yorkshire fog (*Holcus lanaatus*), California thistle (*Cirsium arvense*) and buttercup (*Ranunculus* spp.), the latter being an indicator of high soil moisture (Nelms et al., 2007). Gorse (*Ulex europaeus*) and broom (*Cytisus scoparous*) can also be found everywhere around Tiromoana Bush, from the valley bottoms, hill sides and hill tops (Figure 3-3). Additionally, grazing has not been entirely excluded from the area. Although the site is fenced and domestic grazing animals excluded, signs of browsing by

deer can still be found on native trees inside the reserve. Bush fires can also be a threat to conservation and to restoration of the local native vegetation. The presence of pine trees and hiking tracks in the vicinity increase the risks of natural or intentional fire ignition.

Figure 3-2 Satellite image of Tiromoana Bush and surroundings, North Canterbury. Source: Esri, DeLorme | DigitalGlobe, GeoEye, CNES/Airbus DS | Esri, HERE.

Figure 3-3 Rank Grass study site in Tiromoana Bush. Top picture: prior to trail set up, in February-2012. Bottom picture: trial being set up in October-2012.

- *Willows Reserve*

The Willows Reserve (-43.47°, 172.32°, 128 m a.s.l.) is located on the lower catchment of the Waimakariri River, mid-Canterbury Plains, and covers approximately 27.8 ha of former agricultural and pastoral land, that is now part of a restoration project being carried out by Environment Canterbury (ECan) as an attempt to restore the biodiversity of the area (Figure 3-4). Average annual rainfall is between 600-700 mm, averaging below 400 mm in the summer. The region normally experiences long dry spells (periods of at least 15 consecutive days none of which receives more than 1 mm of rain) during summer. Average daytime temperatures in the summer range from 21°C to 32°C, whereas daytime temperatures in winter are cooler, ranging from 7°C to 14°C and frosts are common (Figure 3-11).

Prior to European settlement the vegetation of this site would most likely have comprised tussock grassland, shrubland and open forest. Nowadays, the area is farmed and it currently offers many challenges to restoration and protection of native vegetation. The land on which the study site is located has been cultivated and grazed for the last 100-plus years, and it still is surrounded by farms on which grazing exists. Several exotic plant species occur in the area, including gorse (*Ulex europaeus*), broom (*Cytisus scoparius*), and yellow lupin (*Lupinus arboreus*), exotic grasses such as browntop (*Agrostis capillaris*), and herbs such as clover (*Trifolium* spp.). Exotic trees are also found around the site, including white poplar (*Populus alba*) and pine (*Pinus radiata*). The reserve includes two endemic species of kowhai (Fabaceae): *Sophora microphylla* (tree) and *S. prostrata* (shrub). Low soil water levels throughout the year, shallow and compacted soils, strong winds during summer and the presence of exotic grasses, together with grazing by rabbits and hares, are the main challenges for restoration efforts in the Willows Reserve (Figure 3-5).

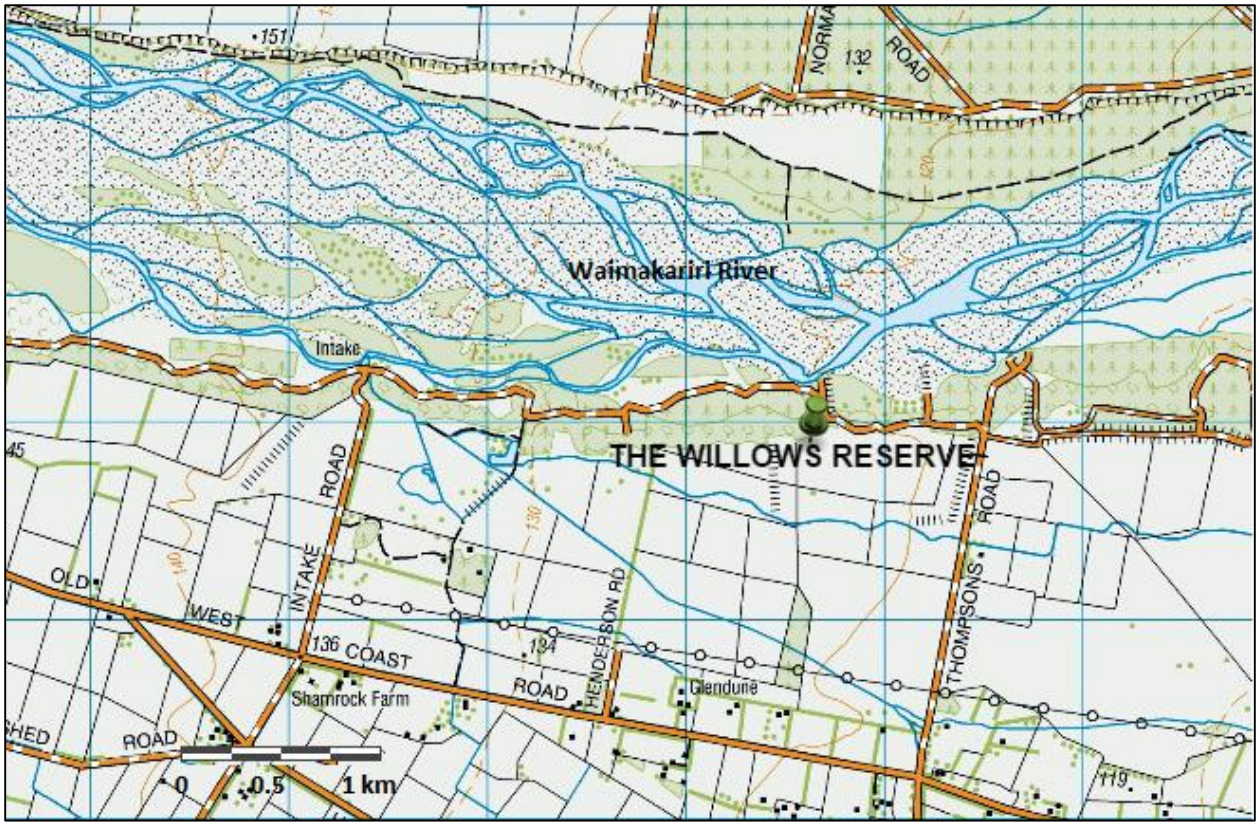


Figure 3-4 Topographic map of the Willows Reserve and surroundings, North Canterbury. Source: Esri, DeLorme, MapmyIndia, © OpenStreetMap contributors | Eagle, LINZ.

Figure 3-5 Rank Grass study site in The Willows Reserve in March-2013.

Dierickx Farm

The third Rank Grass site was set up on Dierickx Farm (-43.85° 170.56°, 730 m a.s.l.). This 394 ha property is located on the eastern shores of Lake Tekapo in the Mackenzie Basin (Figure 3-6). The climate is semi-continental, with warm dry summers and temperatures ranging from 8.5°C to 21°C. Winters are cold, with mean temperatures extending from -3.3°C to 6.0°C. It is typically a dry climate, with a yearly variation in the mean annual precipitation levels (700 to 800 mm), mostly concentrated in the autumn and winter months (Figure 3-11). Restoration efforts are hindered at this site due to strong winds and direct solar radiation that intensify soil water evaporation and low soil moisture, especially during summer. Native seedlings are also exposed to extreme temperatures in winter, including frost and snow. The area is now covered by a rank growth of exotic grasses and herbs, remnants of decades of pastoral and agricultural activities. Hawkweeds (*Hieracium* spp.), a common species elsewhere in the Mackenzie Basin, are not very common on Dierickx Farm, but browntop (*Agrostis capillaris*) is dominant across the property (Figure 3-7).

Figure 3-6 Topographic map of Dierickx Farm and surroundings, Mackenzie Basin. Source: Esri, DeLorme, MapmyIndia, © OpenStreetMap contributors | Eagle, LINZ.

Figure 3-7 Rank Grass study site on Dierickx Farm in October-2012 (top) and April-2013 (bottom).

3.1.2 Degraded Short Tussock Grassland

Two trials were established at Glenmore Station (Irrigation and Grazing trials) located on the western side of Lake Tekapo, on the edge of the Mackenzie Basin, South Canterbury (Figure 3-8). The dryland zone in the Mackenzie Basin was thought to be covered by shrubland and open forests that were transformed into grasslands by Maori settlers mostly through burning (McGlone, 2001). Much of the area is now covered by exotic grasses and weeds, infested by introduced rabbits that now comprise degraded tussock grasslands. Cessation of grazing in some lowland short tussock grasslands has led to dominance by a few of the more vigorous exotic species and to reductions in native and total species richness (Meurk et al., 1989; Lord, 1990). Nevertheless, high country vegetation is dominated by native plants, especially tussocks, a range of exotic plants are also present including herbaceous and woody species. Decades of grazing and farming, combined with weakly structured and fine soil particles (see Appendix: Soil Physical Analyses – Soil Classification), and the exposure of the Mackenzie Basin to strong, north-west winds have predisposed the bare soil to wind erosion and soil compaction (Boswell & Espie, 1998).

The Irrigation trial (-43.90° 170.39°, Figure 3-9) was established in the farm block called Sardine, and the Grazing trial was established in the farm block called Sunday (-43.91° 170.42°, Figure 3-10), at Glenmore Station, at approximately 900 m above sea level. Data from adjacent weather stations indicate the climate of Glenmore Station is semi-continental, with warm dry summers and cold winters. Average annual precipitation in Godley Peaks, the neighboring station, is 762 mm, though some years rainfall can be lower than 400 mm (Norton, 2006). Mean summer temperatures range from 8.5°C to 21.0 °C. Snow is common in winter, normally at altitudes above 1000 m, though it can extend down to Lake Tekapo at times, and persist for several months. Winter mean temperatures can vary from -3.3 °C to 6.0 °C in July (Figure 3-11). Original (pre-human) native vegetation cover on Glenmore Station is limited, covering only 3.5% of the property, while 46% of the land is dominated by induced snow tussock and short-tussock grassland, and another 37% of the property is comprised of rock and scree. Although some of the native grasslands have been modified and lost many species, Glenmore Station has been identified as significant for conservation due to the presence of some indigenous species known to be rare and under threat (Norton, 2006).

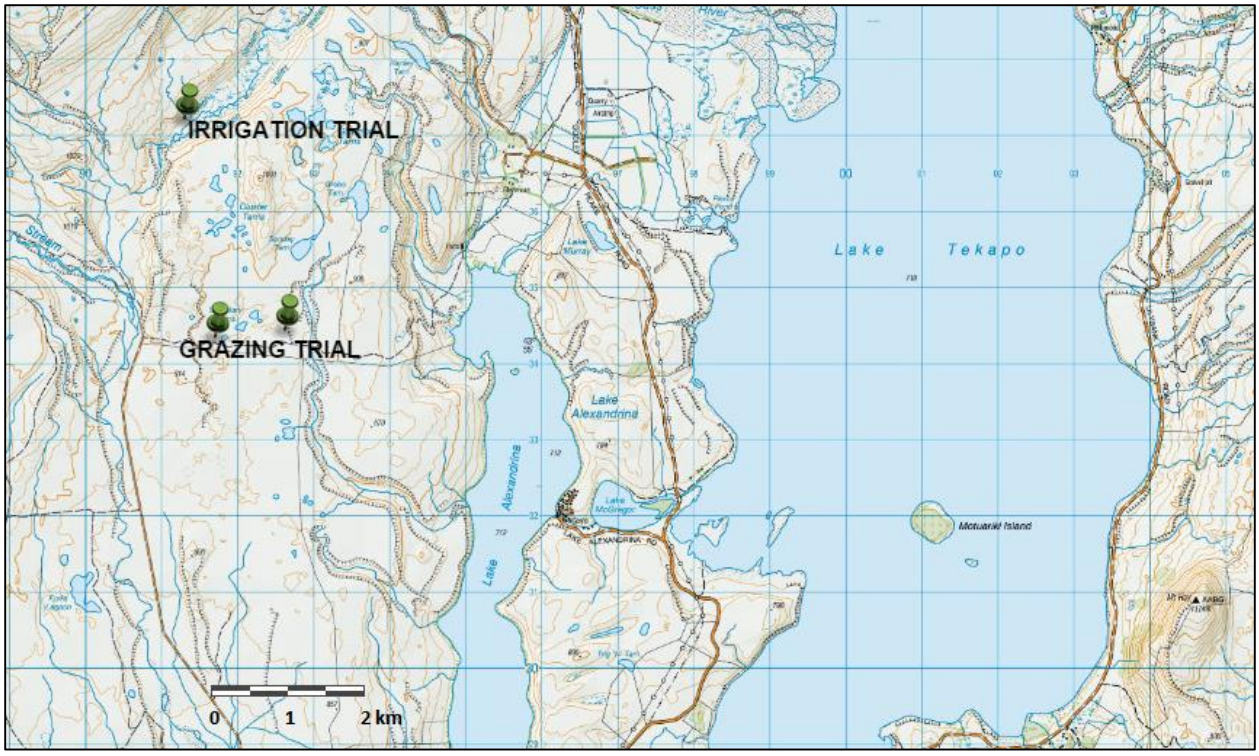


Figure 3-8 Location of the Degraded Short Tussock sites (Irrigation and Grazing trials), Mackenzie basin. Source: Esri, DeLorme, MapmyIndia, © OpenStreetMap contributors | Eagle, LINZ.

Figure 3-9 Irrigation study site on Glenmore Station, Tekapo in March 2014.

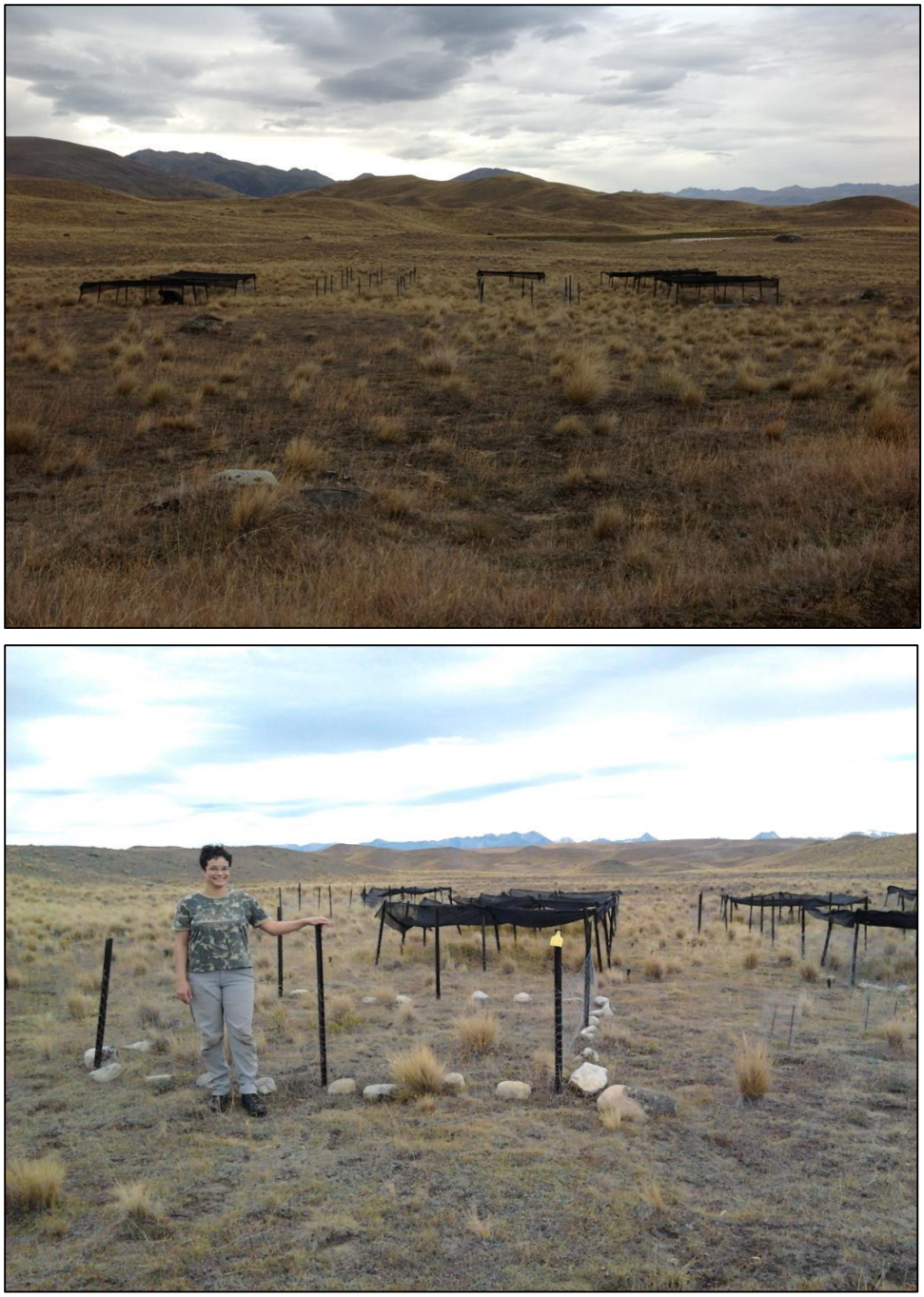


Figure 3-10 Grazing study site on Glenmore Station, Tekapo, in March-2013 (top) and March-2014 (bottom).

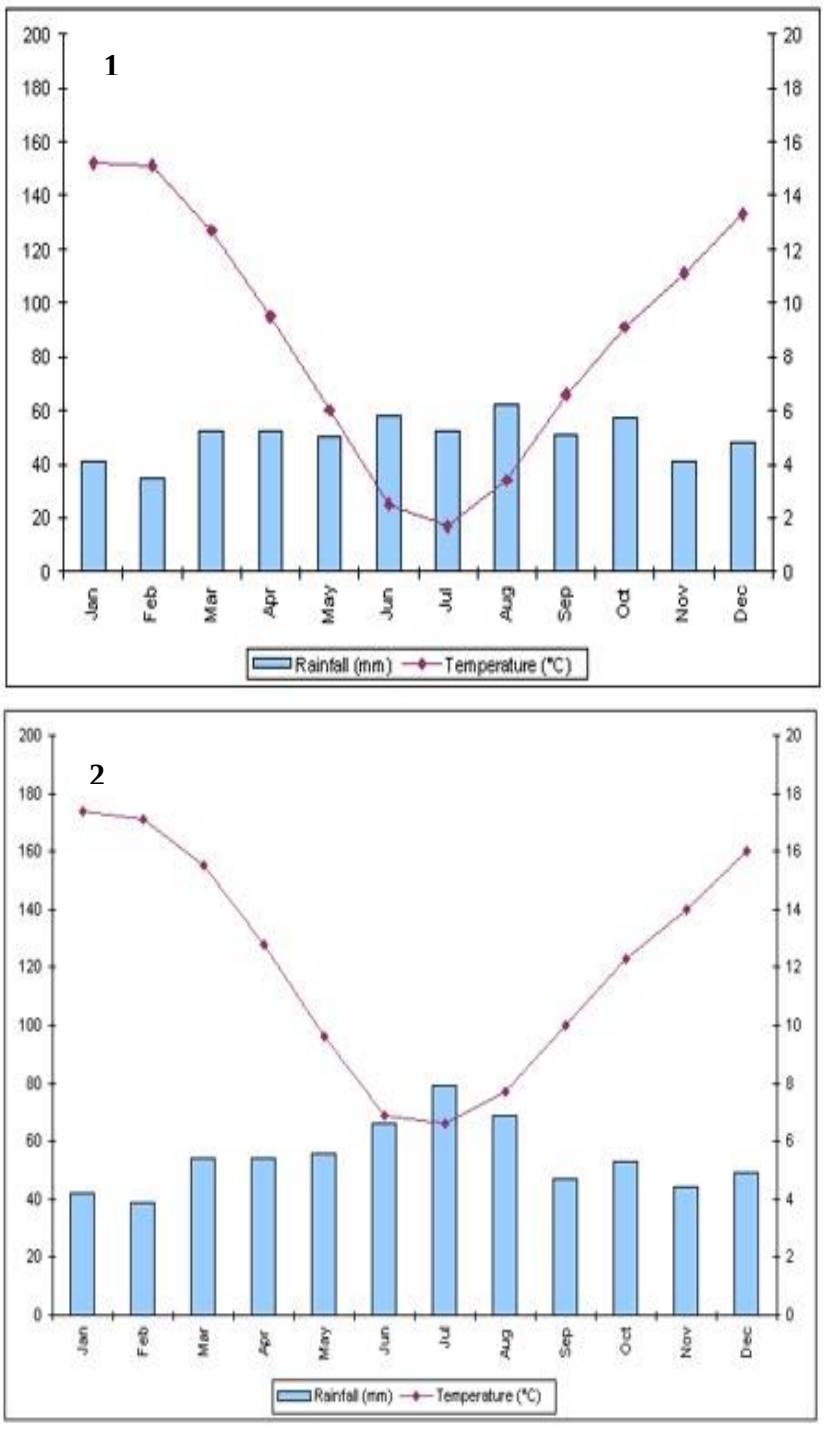


Figure 3-11 Long-term (1971-2000) mean annual rainfall and temperature graphs for Lake Tekapo (1) and Christchurch (2) regions. Source: www.niwa.co.nz.

3.2 Weather Data

The monthly weather data for all five study sites were downloaded from The National Climate Database (www.cliflo.niwa.co.nz) for the duration of the field work (December-2012 to April-2014). The data sources were weather stations located in a 5 to 20 km radius of the study sites. The averages, standard deviations, maximum and minimum values were calculated for 17 months based on the monthly averages.

- **Tiromoana Bush:** Waipara West Ews weather station, approximately 16.6 km west from Tiromoana Bush study site.
- **Willows Reserve:** Christchurch Airport weather station, approximately 18.1 km southeast from the study site.
- **Glenmore Station Sites and Dierickx Farm:** Lake Tekapo EWS and Lake Tekapo Air Safaris weather stations, approximately 12 km from Glenmore Station and 20.4 km from Dierickx Farm.

3.3 Treatment Description and Plot Layout

3.3.1 Rank Grass sites

Seven treatments were randomly implemented in the Rank Grass trials:

- Cultivation and shade (C+S);
- Cultivation-no shade (C-S);
- Herbicide and shade (H+S);
- Herbicide-no shade (H-S);
- Mulch and shade (M+S);
- Mulch-no shade (M-S); and
- Control.

The number of replicates of the treatments were five at Dierickx Farm and six in Tiromoana Bush and The Willows. The plots were 3.5 x 3.5 m area, and 3.5 m apart with a buffer area of 2.0 m between the plots and the surrounding rabbit-proof fence.

- **Herbicide Application**

The wide-range, non-selective ORION® Glyphosate 360[1] herbicide combined with a broad spectrum foliage herbicide Buster Herbicide Weed Killer was sprayed approximately one month before planting. The concentration used was 200 ml of Glyphosate and 75 ml of Buster in a 15 litre knapsack for manual spraying. Glyphosate 360 Herbicide is a water-soluble herbicide for non-selective control of many annual, aquatic and perennial weeds. Buster is a broad-spectrum foliage herbicide for the control of annual and perennial grasses and broadleaf weeds including clovers and cleavers. Both herbicides are biodegradable and break down easily with no adverse effects on either water or soil microorganisms. They are inactivated upon contact with the soil and are safe around the roots of established shrubs and trees, as long as the recommended concentration is applied. Reapplication of the herbicide was necessary at Tiromoana Bush in March-2013, and again in September-2013, where treated plots were constantly recolonized by exotic grass and weed species that did not seem to be affected by the product (*Cirsium arvense* - thistle), hence the constant regrowth and multiple herbicide applications (Figure 3-12 and Figure 3-13). As for the other two Rank Grass sites, the treated plots were also re-infested by exotic weed and grass species on the course of the research, but the sward did not grow at the same rate or speed as in Tiromoana Bush, and hand weeding was enough to control re-infestation (Figure 3-14 and Figure 3-15).

[1] 360 g/l of glyphosate as the isopropylamine salt in the form of a soluble concentrate.

Figure 3-12 Plot in Tiromoana Bush five months after first herbicide application covered by California thistle (*Cirsium arvense*). Flagging tape is to indicate where seedlings were planted.

Figure 3-13 Cultivated plot in Tiromoana Bush in March/2013. In the picture, a *Pittosporum tenuifolium* seedling covered by the exotic rank grass.

Figure 3-14 Plot in the Willows Reserve in September-2013, ten months after first spraying, covered by clover (*Trifolium pratensis*). Restoration plants in the background.

Figure 3-15 Cultivated plot in Dierickx Farm in September-2013, ten months after start of the experiment. Grass is slowly growing back.

- **Shade**

The shaded treatment comprised a 3.5 m² shade-cloth with 75-65% light permeability placed above the plots at 1.5 m from the ground, held up by metal Y-posts at each corner and one in the center of the plot (Figure 3-16). The shade cloths provided an artificial shelter to the seedlings, mimicking what the canopies of shrubs and trees might have provided.

Figure 3-16 Plot covered with shade cloth and newly-planted seedlings. The grass was sprayed in this plot a month earlier. The Willows Reserve.

- **Mulch**

The mulch treatment comprised of a protective cover of a porous black plastic mesh placed over the previously herbicide-sprayed grass, stapled to the ground along with another cover of organic coconut fiber mat on top to reduce direct heating of the soil. The mulch needed to be stapled to the ground to prevent it from being displaced by wind (Figure 3-17). Mulching is often used to control erosion, increase soil moisture, and to suppress germination of weed seeds from the soil seed bank (Stevenson & Smale, 2005).

Figure 3-17 First step (a): Permeable black plastic mesh covering herbicide-sprayed grass; Second step (b): coconut fiber mat placed on top of the plastic mesh and stapled to the ground of the plot. The Willows Reserve.

- **Cultivation**

The cultivation treatment involved the use of a hydraulic rotary hoe for tillage after herbicide application a month earlier. It stirred and pulverized the top 20 cm of the soil surface before planting. The advantage of this type of cultivator is that they are designed to disturb the soil in careful patterns. Seedlings were then planted immediately after the plots had been cultivated.

3.3.2 Degraded Short Tussock sites

- **Irrigation Trial**

The Irrigation Trial, located in the Sardine paddock of Glenmore Station, was completely fenced off against grazing animals, including lagomorphs. The plots were 3.5 x 3.5 m in area, and 3.5 m apart, with a 2.0 m buffer area between the fence and the nearest plot. The treatments consisted of a combination of shade cloths and irrigation (4 treatments), with six replicates (24 plots in total), placed randomly around the study site:

- (I-S-) Control;
- (I+S+) Irrigation and shade (Figure 3-18);
- (I-S+) No-irrigation and shade;
- (I+S-) Irrigation, no-shade (Figure 3-19);

The irrigation system was composed of small sprinklers staked to the ground in the center of the irrigated plots. A 5,000 liter tank was installed near the stream that runs through this part of the property (Joseph Stream), at approximately 250 m distance from the study site, and at 936 m of altitude (the study site is at 918 m). A 20 mm 900 KPA/130 PSI pipe was installed between the stream and the tank, and a 32 mm 800 KPA/115 PSI pipe transported the water from the tank to the study site by gravity. The pipes were connected to a digital controller located inside the study area, and smaller (13 mm in diameter) pipes distributed the water among the plots by capillary pressure. Capillary rubber tubes were connected from the 13-mm pipes to the sprinklers in the center of the irrigated plots. Irrigation time was set up at 6:00 and 18:00, daily, for 15 minutes each round, throughout the summer months of 2012/2013 and 2013/2014. The irrigation system

was turned off and the tank and pipes drained during autumn and winter to avoid damage to the pipes due to frost.

Figure 3-18 *L. scoparium* and *O. leptophyllus* seedlings in an irrigation and shade (I+S+) plot, in February-2013 (sprinkler on the right side of the picture). Irrigation Trial.

Figure 3-19 *L. scoparium* and *O. leptophyllus* seedlings in an irrigation, no-shade (I+S-) plot, in February-2013 (sprinkler on the bottom-right side of the photo). Irrigation Trial.

- **Grazing**

Four treatments with eight replicates each were randomly established at two separate blocks within the Sunday paddock on Glenmore Station for the Grazing trial. The blocks were approximately 1 km apart, but soil physical and chemical analyses proved that the two blocks were similar in terms of soil nutrient levels and soil type, enabling them to be analyzed as one study site (see Appendix: Soil Analyses). The treatments were as follows:

- (G+S-) Control;
- (G+S+) Grazing (unfenced) and shade;
- (G-S+) No grazing (fenced) and shade
- (G-S-) No grazing (fenced) no shade.

One block had three (3) replicates of each treatment (12 plots) and the second block had five replicates (20 plots). The plots were 3.5 x 3.5 m in area, separated from each other by a 3.5 m buffer area. The Grazing site was not fenced off, except for the selected no-grazing plots, to test the effects of grazing/herbivory on the establishment and growth of the native woody seedlings.

3.4 Species Selected

The native woody tree species were selected according to their provenance and habitat specifications for easier adaptation to the study sites' climates and the maintenance of genetic integrity. *Pittosporum tenuifolium* and *Kunzea robusta* were planted in Tiromoana Bush and in The Willows Reserve. *Leptospermum scoparium* and *Ozothamnus leptophyllus* were planted at Dierickx Farm and on the Degraded Short Tussock sites. The species selection for these sites was also based on what has historically been recorded as their original habitats (Connor & Edgar, 1987; Schönberger, 2002; Wardle, 2002; Dawson et al., 2011).

3.5 Planting and Plot Layout

Tiromoana Bush and The Willows Reserve:

- Seven treatments with six replicates = 42 plots (Figure 3-20 and Figure 3-21);
- 504 large (20-40 cm tall) and 504 small (< 5 cm tall) seedlings of *Kunzea robusta* and *Pittosporum tenuifolium.*

Dierickx Farm:

- Seven treatments with five replicates = 35 plots (Figure 3-22);
- 420 large (20-40 cm tall) and 420 small (> 5 cm tall) seedlings of *Leptospermum scoparium* and *Ozothamnus leptophyllus.*

Irrigation:

- Four treatments with six replicate = 24 plots (Figure 3-23);
- 288 large (20-40 cm tall) and 288 small (> 5 cm tall) seedlings of *Leptospermum scoparium* and *Ozothamnus leptophyllus.*

Grazing:

- Four treatments with eight replicate = 32 plots (Figure 3-24);
- 384 large (20-40 cm tall) and 384 small (> 5 cm tall) seedlings of *Leptospermum scoparium* and *Ozothamnus leptophyllus.*

Large and small seedlings were planted on different sides of the plot, as close to the center as possible to avoid edge effect on seedlings (in the case of the shaded treatments). Seedlings were planted approximately 250 mm apart from one another as shown in Figure 3-25. The use of large and small seedlings was designed to test the effect of the different treatments on different stages of plant establishment, with small seedlings representing plants that had just germinated and large seedlings the plants that would more typically be used in restoration plantings. Unfortunately, the small seedlings experienced very high mortality (> 80%) in the first season at all five study sites and have been excluded from the analyses.

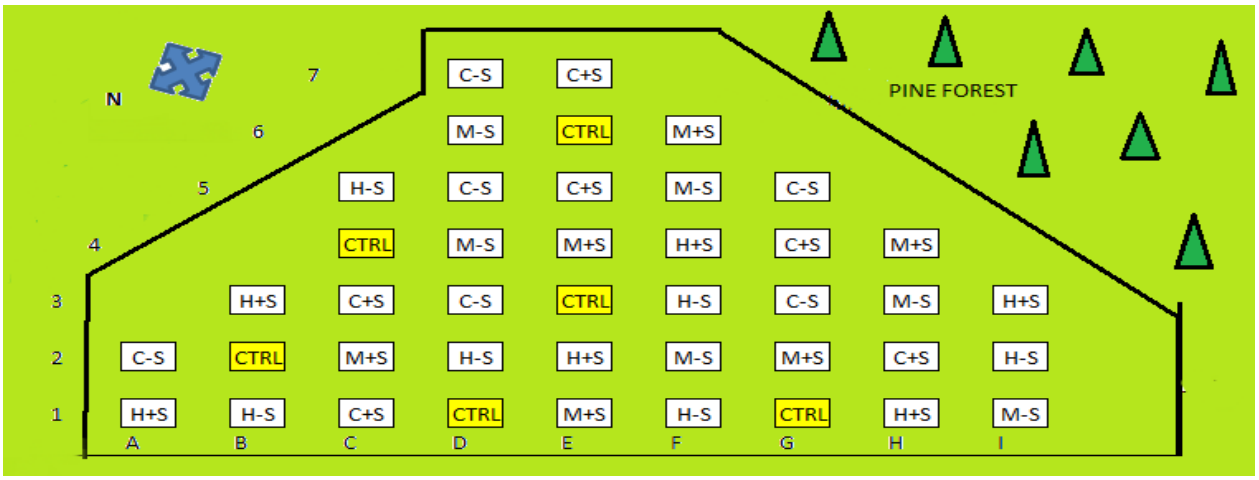


Figure 3-20 Plot layout of Tiromoana Bush study site, Rank Grass trial. Northern Canterbury.

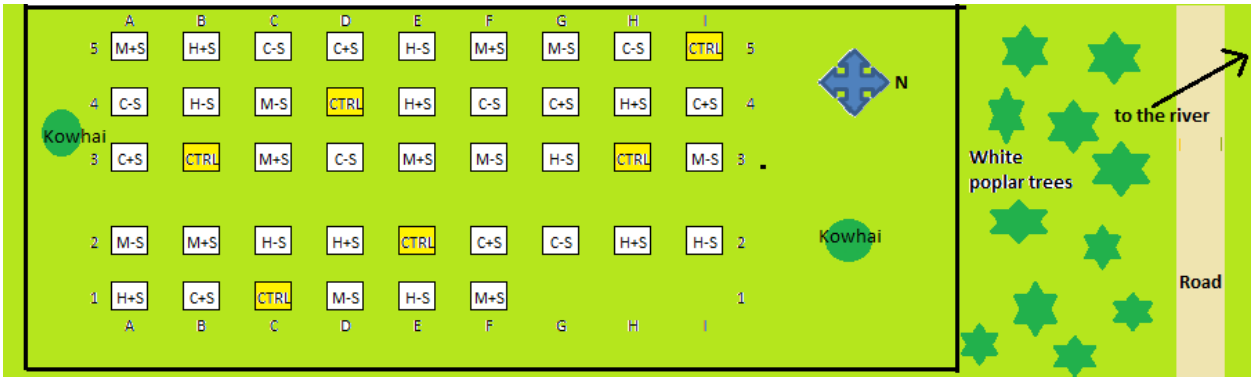


Figure 3-21 - Plot layout of The Willows Reserve study site, Rank Grass trial. Northern Canterbury.

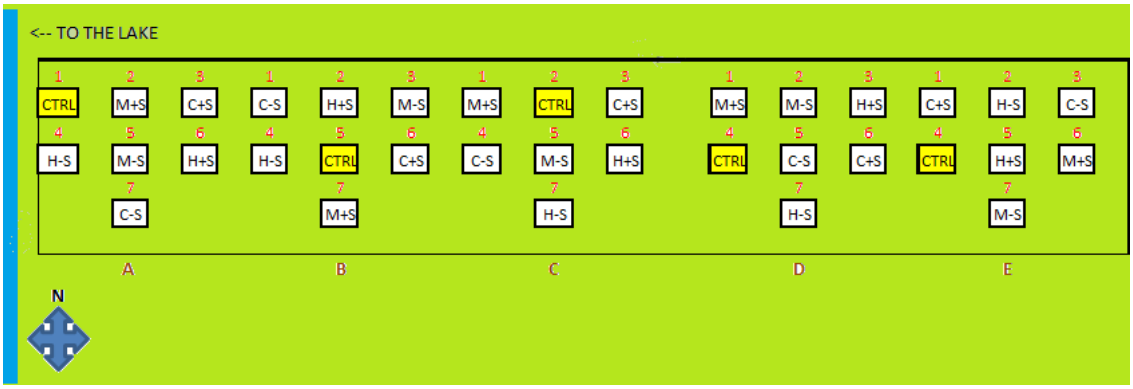


Figure 3-22 Plot layout of Dierickx Farm study site, Rank Grass trial. Mackenzie Basin.

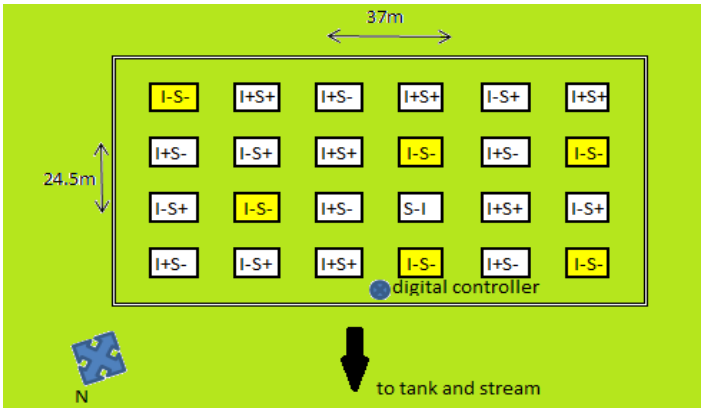


Figure 3-23 Plot layout of the Irrigation site, Degraded Short Tussock trial. Mackenzie Basin.

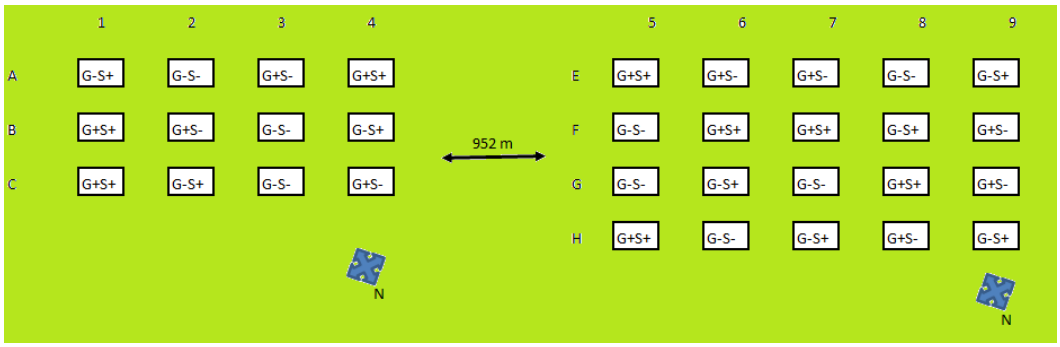


Figure 3-24 – Plot layout of the Grazing site, Degraded Short Tussock trial. Mackenzie Basin.

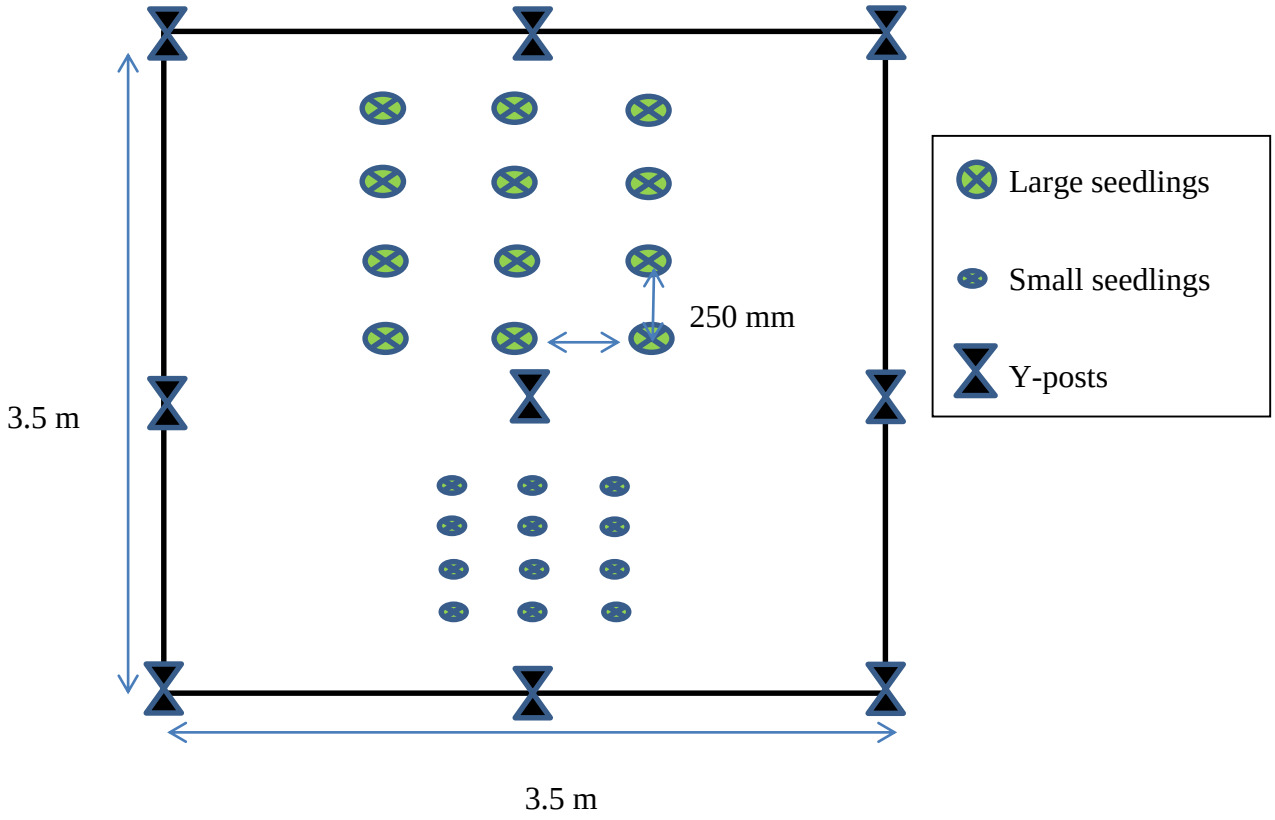


Figure 3-25 – Plot diagram and the distribution of the plants.

3.6 Field Methods

3.6.1 Counting of Survivors and Height Measurements

Seedling stem height (height from ground to the apical meristem) was measured in centimeters with an 8.0 m x 28.0 mm aluminum BizLine tape measure. The first year height measurements were obtained at planting (December-2012) and in April-2013, concomitantly with counting of survivors at the end of the first summer. The second year height measurements started in October and November-2013, and were repeated in April-2014, marking the end of the field experiment. Counting of survivors and height measurements were not undertaken during the winter of 2013. Height measurements of plants that had lost part of their apical meristem (dried, fell off, broke, or was browsed) were taken from the ground to the top apical meristem on the highest green branch attached to the main stem.

The relative height increment (RHI, Equation 3-1) was calculated for each plant, per site, per treatment type and per species, at the end of the last measurement and according to the formula used by Evans (1972) and Causton (1991):

Equation 3-1

$$RHI=ln(H_f)-ln(H_o)$$

where RHI is the natural logarithm (ln) of differences between the final seedling height measurement (H_f) and the height of the seedling at planting (H_o). According to Pearcy et al. (1989), calculating RHI is a useful index of plant growth as this technique eliminates the errors in calculation of growth rates that can be caused by different initial sizes (Kozlowski et al., 1991; Van den Driessche, 1992); therefore, making the comparisons in relative growth rates among different seedlings more accurate in determining which seedlings grow the best (Brand, 1991; Causton, 1991).

Percentage of survival (Equation 3-2) was calculated for each plant, per species and per treatment replicate separately by dividing the number of living seedlings at the end of the

experiment (*Nf*) by the initial number of seedlings in the beginning of the trial (*No*), then multiplying the result by 100, to transform it into a percentage:

Equation 3-2

$$Survival\ (\%) = \frac{Nf}{No}\ x\ 100$$

3.6.2 Chlorophyll Fluorescence Measurement

In this research, due to the limited number of seedlings for the experiment, it was decided to measure chlorophyll fluorescence of each seedling as a way to quantify the physiological state of the photosynthetic apparatus of the plants (Baker, 2008), therefore, providing a measurement of stress of the native seedlings under each treatment. Chlorophyll fluorescence reading, or quantum yield, is a non-destructive physiological measurement that can be performed on living tissue (leaves) and at the site (no harvesting of plants necessary). A photosynthesis yield analyzer, the MINI-PAM Portable Chlorophyll Fluoromter® Heinz Walz GmbH was used to measure the fluorescence readings (Genty-parameter in Equation 3-3) of the seedlings in the Rank Grass trials only, due to the fragility of the equipment and because the Rank Grass sites were easily accessed by car without bumpy and rough four-wheel driving. Detailed explanation on how to use the MINI-PAM machine and the type of readings provided can be obtained online (http://www.walz.com/downloads/manuals/mini-pam/mini-pam_screen.pdf). The MINI-PAM is the miniaturized fluorometer developed to determine the effective quantum yield (Y-value) of photosynthetic energy conversion, ΔF/Fm' or Genty-parameter:

Equation 3-3

$$YIELD\ =\ Y/1000\ =\ (M-F)M\ =\ \Delta F/M\ =\ \Delta F/Fm'$$

The MINI-PAM applies pulse-modulated measuring light for selective detection of chlorophyll fluorescence or quantum yield or Y-value. The actual measurement of the photosynthetic yield is carried out by application of just one saturating light pulse which briefly suppresses photochemical yield to zero and induces maximal fluorescence yield. The given Y-value is then

calculated and displayed on the MINI-PAM LC screen. This measuring principle is patented (DE 35 18 527) and licensed exclusively to the Heinz Walz GmbH.

- *Preparation of the samples:*

Fluorescence readings can be affected by moisture and the MINI-PAM might provide inaccurate Y-values if plant leaves are somewhat wet. Readings were therefore preferably taken after at least two days of no rain and normally after 8 am, when moisture from dew had already dried out. Healthy-looking leaves were selected whenever possible (mostly bright green leaves, with no or few dark spots, or dry edges), placed one dark-leaf clip (DLC-8® Heinz Walz GmbH) on one leaf per plant, and the readings taken 15 minutes later. The DLC-8® weighs approximately 4 grams and can be attached to most types of leaves without causing any injuries. The clips are equipped with a miniature sliding shutter which prevents light from accessing the leaf during a dark-adaptation period. Proper dark-adaptation is essential for determination of the maximal quantum yield (Fv/Fm). The shutter is then slid for the actual measurement only, when exposure to external light is prevented by the fiberoptics (Figure 3-26). After the 15-min elapsed time, the fiberoptic cable attached to the MINI-PAM is connected to the dark-leaf clip on the plant's leaf, the sliding shutter pulled open, and the measurement made. This procedure was repeated on every living plant at each study site and the Y-values displayed on the LC screen recorded. For species such as *Kunzea robusta*, *Leptospermum scoparium* and *Ozothamnus leptophyllus*, whose leaves are small, several leaves had to be gathered in a bundle for the placement of the dark-leaf clip, certifying that no ambient light could come through any apertures formed by the bundled leaves, and that the sliding shutter was firmly closed without any leaves jamming it (Figure 3-27).

Fluorescence readings were performed the first time one month after planting, in January-2013, to avoid the influence of transplantation-stress on the Y-readings of the plants. Further measurements were taken in March or April-2013, October-2013, January-2014, and March or April-2014.

Figure 3-26 Step-by-step of chlorophyll fluorescence measurement. Clockwise: MINI-PAM Portable Chlorophyll Fluoromter® Heinz Walz GmbH; DLC-8 dark-adaption leaf clip on a *Pittosporum tenuifolium* plant; seedlings with the DLC-8 clips during the dark-adaptation period (approx. 15 minutes); fiberoptics engaged in to the DLC-8 clip for the Y-value reading.

Figure 3-27 A DLC-8 clip on several small leaves of a *Kunzea robusta* seedling.

3.7 Laboratory Methods

3.7.1 Gravimetric Soil Water Content Monitoring

Gravimetric soil water content or soil moisture (Θ %) was monitored from the establishment of the trials in December-2012, then again in January-2013, March or April-2013, October-2013, January-2014 and March or April-2014. Soil samples were collected from all five study sites usually when chlorophyll fluorescence readings were undertaken (Rank Grass sites only). Samples of 100 g of soil from each plot, at approximately 15 cm deep, were collected and immediately deposited into plastic bags, subsequently sealed with duct tape, identified (study site, date of collection, plot number and treatment type), and transported from the field to the laboratory in a chilly bin in order to reduce moisture loss during transport. Once in the laboratory, empty metal cups (10 cm in diameter and 5 cm deep) were weighed ("cup" weight). Then, each sample bag was emptied in to the metal cups and weighed on a 0.001 g precision automatic scale ("wet soil" weight). Weighed samples were later kept in an oven at 105 ± 5.0ºC for at least 24 hours. The cups and the dry soil were then weighed again ("dry soil" weight) and the soil-water content was calculated using the formula:

Equation 3-4

$$\Theta(\%) = [(Ww - Wd)/(Wd - Wc)]x100$$

Where Ww is the weight of the "wet soil" plus the weight of the "metal cup"; Wd is the weight of the "dry soil" plus the weight of the "cup"; and Wc is the weight of the "cup". Soil water content per treatment type was a measure of percentage of water in, approximately, 100 g of soil.

3.7.2 Carbon Isotope Analysis ($\delta^{13}C$)

Carbon Isotope analysis, or Carbon isotope signature ($\delta^{13}C$), an *ex situ* destructive physiological test, was chosen to be performed on dried leaf samples of the surviving plants from all five study sites, per species and per treatment, at the end of the field experiment. Carbon isotope signature of plant tissues can reflect long-term plant responses to different environmental conditions and stresses (Vogel et al., 1993) through the assessment of water use efficiency in plants (Tognetti et

al., 2000; Adiredjo et al., 2014). Due to limited funding, but being aware of the need for adequate replication, it was decided to have at least three (03) replicates of each species, per treatment type, from all five study sites. However, for some treatments at some sites, the high mortality rate meant the ideal number of replicates was not always reached. Leaf samples were collected, placed in paper bags and dried in an oven for 24 hours at 60° C. The oven-dried leaves were then pulverized in a mechanical miller. Approximately 1.0 g of pulverized leaves of each individual plant and replicates, per species and per treatment, was then put in small plastic flasks and sent to the Faculty of Science and Engineering Services at the University of Waikato for carbon isotope analysis. For details on the methods used for Carbon Isotope Analysis performed by Waikato Stable Isotope Unit (WSIU), see http://sci.waikato.ac.nz/research/centres-and-units/isotope.

3.7.3 Soil Physical Properties

Approximately 300 g of soil within 15-20 cm depth were collected from six different and randomly chosen spots at all five sites for soil physical analyses. The soil samples underwent a series of geomechanical tests for soil type classification. Soil type influences soil moisture levels; hence, it is strongly related to how plants respond to the environment as a consequence of soil-water availability. The tests were performed in the Geomechanical Laboratory of the Civil Engineering Department, at University of Canterbury, following instructions found in Bardet (1997) and New Zealand Standard Methods of Testing Soils for Civil Engineering Purposes (or NZS 4402:1986):

1. Dry Sieving test for Grain Size and Grain Size Distribution;
2. Sedimentation test using a Hydrometer;
3. Wet sieving test;

These tests were performed only once, at the beginning of the experiment, since no significant changes in the soil physical properties were expected to take place within the duration of the trials. The results of the geomechanical tests and soil classification are presented in the Appendix: Soil Physical Analyses – Soil Classification.

3.7.4 Soil Chemical Properties

Soil samples were collected before planting from the study sites for nutrient tests. Approximately 300 g of soil within 15-20 cm depth collected from six different and randomly chosen spots at all five sites and put in plastic bags, sealed with duct tape, identified (study site and date of collection), and sent to Hill Laboratories for analysis. Ten soil nutrient tests were performed for this research following standard methods (as described in the report provided by Hill Laboratories and displayed in the Appendix, section 8.2.2, Figure 8-6).

Soil chemical analysis was performed for characterization of the nutrient levels of the study sites only. The results were not used in any statistical analyses or for assessing the responses of the native seedlings to the treatments and are presented in the Appendix: Soil Chemical Analyses.

3.8 Statistical Analyses

In this section, a brief introduction to Bayesian inference statistics is presented. Additionally, the construction of the statistical models is described to explain how each parameter was analyzed, separately, per study site and per species, as well as the method used for comparing the strength of each treatment on:

- Survival;
- Relative Height Increment;
- Chlorophyll Fluorescence (Rank Grass sites only);
- Soil Moisture; and
- Carbon Isotope Signature.

The main reason for choosing Bayesian statistics over the more traditional frequentist, or classical, approach was the nature of the data from some of the study sites. Mortality was high at most sites, and many plots had no plants left by the end of the experiment, resulting in some treatments having no living plants to analyze. The assumptions of running an analysis of variance (ANOVA) and calculating p-values are, first of all, large sample sizes (asymptotics) to avoid bias, that the data has a normal distribution and that there is homogeneity of variance. These assumptions could not be fulfilled by some of the data used in the experiments. When firstly it was attempted to analyze the data using mixed effect linear regression models (LME), generalized linear models (GLM) and Tukey Pairwise tests in the classical approach, some outputs failed to provide meaningful p-values.

Since Bayesian inference can be applied to any sample size (Kéry, 2010), it was decided to use one statistical approach for the entire experiment so as to maintain a coherent analysis of the results and to be able to undertake comparisons across study sites in search of larger-scale patterns in the results. The mixed effects logistic models fitted in a Bayesian framework, for example, are appropriate for modeling categorical responses such as survival (Aliyu et al., 2014). The Bayesian approach allows the user to define the statements to be considered in a hypothesis rather than restricting the analysis to bilateral comparisons such as pairwise tests. In the frequentist inference, p-values are probabilities of rejecting the null hypothesis – H_0 – whereas

the Bayesian P values are probabilities that the statement is true given the observed data (Kéry, 2010). It is not the intention, at any point, to use this work as a critique of the classical statistical approach. Nor is it intended to use the present research to vouch for Bayesian statistics over frequentist, but rather to explain the validity of the analyses under discussion by demonstrating how each model was carefully designed to fit the type of data being analyzed. The calculation of the effectiveness of one treatment over another is demonstrated through a Bayesian alternative to the frequentist p-values, in order to draw the conclusions presented later in this thesis.

3.8.1 A brief introduction to Bayesian Statistics

According to the American Heritage Dictionary of the English Language (Morris, 1969), statistics is a mathematical tool used for making probabilistic extrapolations about the behavior of a stochastic system based on observations of certain parameters (samples) involved in that system (population). There are basically two ways of analyzing the parameters in a stochastic system: classical, also known as conventional or frequentist, and Bayesian statistics (Kéry, 2010). Although practical applications of Bayesian statistics have only become common in the last 30 years or so, this approach has been applied in various areas for much longer than this. For example, Alan Turing's (1912-1954) feat of breaking the Enigma code during World War II was based on what it is called now a Bayesian statistical approach (McGrayne, 2011). In both statistical frameworks, the results of the analyses are considered as the general behavior of a stochastic system according to the observed (measured) data and one or several random processes. The difference between classical and Bayesian statistics, however, lies on the fact that in the Bayesian approach, the measured parameters are themselves viewed as unobserved results of random processes. Therefore, the result of a Bayesian analysis is presented as the probability of a certain parameter (e.g. survival) based on the data, the model, and on any known prior, historical, or personal information about the parameter before the experiment was conducted (Kennedy & Hart, 2009; Kéry, 2010). The core concept in this method is Bayes' theorem, which can be expressed as:

Equation 3-5

$$p(H|D) = \frac{p(D|H)x\ p(H)}{p(D)}$$

where p(H) is the prior probability that the hypothesis is correct and p(D) is the probability of obtaining the observed data independently of any particular hypothesis. In other words, the posterior probability that a hypothesis is correct given a set of observed data: p(H|D) (Gilks, 2005; Gelman et al., 2014).

The construction of a statistical model in Bayesian analysis comprises any prior information that exists before the study is conducted (prior probability distribution, p(H)) and the measured data (likelihood, p(D)) to calculate the probability distribution of the desired parameter (posterior probability distribution, p(H|D)). Bayes' Theorem (Equation 3-5) can accept either informative or non-informative (vague) priors. The probability of the parameter when using vague priors is solely dependent on the observed or measured data (Kéry, 2010). Posterior probability distributions are, therefore, a direct measure of the degree of belief it can be put on a parameter, a model, or on a hypothesis. Bayesian inference provides the quantitative measure of the probability that an observed parameter (e.g. growth) responds in a certain way (e.g. measured height) due to certain circumstances (e.g. type of treatment) (Ellison, 2004).

As stated earlier, the Bayesian prior is an expression of degree of belief, and the credibility interval (CI%) is the set of parameter values which together constitute a percentage of the entire range of possible outcomes (probability mass), similarly to the confidence interval used in frequentist statistics, which is not a % of probability, but a set of parameter values (Berger and Berry 1988). Because the posterior distribution is often analytically intractable, a numeral procedure run by WinBugs, Version 1.4.3, the Markov Chain Monte Carlo (MCMC), is used to simulate draws from the posterior distribution, which can then be used to construct posterior means, standard deviations, credibility intervals and other statistics of interest (Kennedy & Hart, 2009). These statistical parameters can then be used as a measure of central tendency of the posterior distribution (or posterior probabilities).

3.8.2 Hypothesis testing: the Markov Chain Monte Carlo method (MCMC)

The Markov Chain Monte Carlo (MCMC) procedure in the Bayesian approach provides a probabilistic comparison of models or hypotheses based on a distribution of possible effect sizes and the nature of that distribution (Kéry, 2010). The open software WinBUGS, Version 1.4.3, runs MCMC simulations (Gilks, 2005) using a Gibbs sampler (Chib & Greenberg, 1995) for

computation of the conditional posterior or alternative hypothesis P(Hi|D). The suggested categorization of degrees of evidence by Raftery (1995), shown in Table 3-1, provides a helpful labeling system for the strength of the calculated posterior distribution of a parameter given a set of data compared to the strength of the alternative distribution of the same parameter based on a different set of data. In the case of the present research, the comparison was made, for example, between strength of one treatment (e.g. herbicide) compared to another treatment (e.g. mulch) on the posterior distribution of seedling survival, or relative height increment, and so on.

Table 3-1 Descriptive terms for strength of evidence corresponding to ranges of P(Hi|D) values as suggested by Raftery (1995). P = strength of the hypothesis *i*, given the data D.

P(Hi|D)	**Evidence**
0.50 – 0.75	Weak
0.75 – 0.95	Positive
0.95 – 0.99	Strong
> 0.99	Very strong

The models were designed to compare the effects of four or seven treatments, depending on the trial, on one measured variable – survival, or growth, etc. Therefore, WinBugs default number of one MCMC chain and 2,000 iterations were used for each model. The model convergence was assessed visually using the autocorrelation graphs also available on the statistical program. Since there was no autocorrelation problem, thinning was not necessary as the convergence of the models was considered "stable" or reasonable for the number of iterations used.

A *post-hoc* analysis to compare two competing hypotheses on WinBUGS program can be performed using the imbedded *step( )* function which creates a Boolean variable that counts the number of times the statement "P(beta1 ≥ beta2)" in the MCMC simulation is true. If beta is any node (e.g. treatment), then *step(beta)* equals 1 if beta ≥ 0, and equals 0 if beta < 0. Consequently, *step(beta1 – beta2)* equals 1 if beta1 – beta2 ≥ 0; that is, if beta1 ≥ beta2. The mean value of a Boolean node (P) is a probability; therefore, P is the probability that a statement is true given the

observed data, so that Bayesian P values closer to one indicate that the hypothesis is well supported by the data (Aliyu et al., 2014).

3.8.3 Setting up the priors

Computation of the Bayes factor (Equation 3-5) depends on the specification of a prior distribution for the effect size parameter that distinguishes the alternative hypothesis from the null hypothesis. These values cover some distribution whose characteristics influence the eventual posterior probabilities (Kass & Wasserman, 1995). The knowledge of a prior distribution of a parameter gives the researcher some concept of the general range, or array of possible values, that the observed parameter can fall into (Masson, 2011). However, it is possible to specify ignorance in a Bayesian analysis in cases where there is no prior information about the parameter (Kéry, 2010). In the models used to analyze the data in this research, it was chosen to specify non-informative priors (or vague priors) as to obtain results (posterior probabilities) solely based on the measured data, similarly to the frequentist approach. By assigning vague prior values, it was necessarily assumed that all treatments had a uniform, uncertain, and similar effect on the parameter to be measured (Ellison, 2004). In other words, the null hypothesis was that there would be no differences among treatments, in the same way to what is assumed when performing a classical ANOVA; therefore, all estimated values calculated by the models were essentially linked to treatment effect.

3.8.4 Assigning priors to distributions on WinBUGS

- *Normal Distribution (WinBUGS function: dnorm)*

dnorm(μ, τ) is the normal distribution with parameters μ and $\tau = 1/\sigma 2$. WinBUGS automatically specifies the normal distribution as mean μ and precision τ, instead of mean and standard deviation σ. The relationship between standard deviation and precision is $\sigma = 1/\sqrt{\tau}$. In practice, a dnorm(0, ε) is used to represent no prior information regarding the data, or ignorance, where ε is a small number such as 0.001. To help improve normality, the data for chlorophyll fluorescence and carbon isotopic signature were log-transformed before running the statistical analyses.

- *Bernoulli Distribution (WinBUGS function: dbern)*

The *Bernoulli trials process*, named after Jacob Bernoulli (1654-1705), is one random process in probability. Basically, it is a mathematical process that describes, for instance, a virtual tossing of a coin. In this context, the *Bernoulli trials process* can explain the probability of a set of data if the latter satisfies the following assumptions:

- Each trial has two possible outcomes: success (1) and failure (0)*;*
- One trial has no influence on the outcome of another trial (trials are independent);
- The probability of success on each trial is p and the probability of failure is $1-p$, where p∈[0,1] is the *success parameter* of the process.

The success parameter of the Bernoulli distribution was used to calculate the probability of survival of the seedlings, per species type, in each treatment. This distribution, in the exponential family, uses the logistic function (i.e., log odds function: $\eta = log\, \mu /1 - \mu$) to map the mean parameter vector μ (survival), to the natural parameter, η:

Equation 3-6 The logistic function

$$\mu = 1/1 + \exp(-\eta)$$

- *Beta Distribution (WinBUGS function dbeta)*

Beta distribution (on WinBUGS - **dbeta[*a*, *b*])** is a distribution family used to describe a dataset that takes up values between 0 and 1; hence, it is adequate for explaining the random behavior of percentages and proportion. The beta distribution was used in the model designed for the analysis of soil water content per treatment, for each study site, since soil moisture was calculated in percentage, with values for the parameters a and b equal 1 as to state a uniform (flat) prior distribution over the interval. By assigning a flat prior distribution, it was assumed that treatment type would have no effect on soil moisture levels (McCarthy, 2007).

3.9 Statistical models

3.9.1 Probability of survival

Since survival is a binary variable that can only take 0 or 1 to represent dead or alive, and to account for the large number of zeros in the survival survey data, it was assumed that the binary presence/absence of seedlings has a Bernoulli distribution with probability *s[i]*, which in turn depends on the (fixed) treatment effect *beta[trt[i]]* and a plot-specific (random) effect *epsilon[plot[i]]* via a logit link function:

$$Y \sim dbern(s)$$

$$logit(s) = beta + epsilon$$

The sampler was initialized with beta = 0 and tau = 1 as it is customary to run several chains starting from various values to confirm convergence. The default output display is the posterior mean and standard deviation (sd), along with the median and 95% credible interval (95% CI). The estimated probabilities presented in the output gave the relationship between treatment type and survival. Treatment effects are the *beta* and they represent the probability of survival of seedlings of one species in each treatment. For example, in the output, the posterior mean of 0.85 of treatment A means that when treatment A is applied, the seedlings will survive, on average, 85% of the time.

Comparison between treatments (P) was performed using WinBUGS *step* function, which calculated the number of times in the simulation that the sentence betaA>betaB is true (beta = treatment type). The posterior probability that one treatment is better than the other was thus obtained after adjusting for the random plot effect and given the observed data. The result was the percentage of times within the simulation that treatment A had higher probability of survival than treatment B, and so on. If P(s.est of treatment A - s.est of treatment B) ≥ 0, then s.est of treatment A ≥ s.est of treatment B. Bayesian P values closer to one indicate the strength of treatment A on the observed parameter survival is higher than that of treatment B.

3.9.2 Relative Height Increment

A Bayesian Mixed-Effects inference was used to relate the observed data (relative height increment or RHI) to treatment type, where RHI was assumed to have a normal distribution with mean *mu* and variance *tau*.

$$Y \sim dnorm(mu, tau)$$

The posterior mean value of RHI *mu[i]* depends on the (fixed) treatment effect *beta[trt[i]]* and a plot-specific (random) effect *epsilon[plot[i]]* via the logistic regression model:

$$mu = beta + epsilon$$

The sampler was initialized with beta = 0 and tau = 0.1. The default display is the posterior mean and standard deviation (sd), along with the median and 95% CI. Comparison between treatments (P) was performed using WinBUGS *step( )* function, following the same principal explained for the probability of survival model.

3.9.3 Soil water content

Soil water content values were given in percentage and an Arcsine transformation of the data was required before running the statistical analyses. This consists of taking the arcsine of the square root of a number. The result is given in radians, not degrees, and can range from $-\pi/2$ to $\pi/2$. The numbers to be arcsine transformed must be in the range -1 to 1. This is commonly used for proportions, which range from 0 to 1 (McDonald, 2009). The arcsine transformed data was then used in the statistical analysis, fitted in a repeated measures model that was developed in Bayesian framework using WinBUGS, Version 1.4.3, to estimate the average soil-water content per treatment type. However, since the results cannot be reported in arcsine-transformed units, the estimated means were back-transformed for the presentation of the results and discussion of soil water content per treatment in percentages (Θ%).

The model in a Bayesian framework was constructed assuming that the observed parameter has a beta distribution with parameters denoted by:

$$Y \sim dbeta(a, b])$$

The expected value (mean) of soil water content per treatment (*SW.est[j]*) is, therefore, a function of the ratio of the two independent, random variables:

$$SW.est = \frac{a}{(b + a)}$$

Where a = b =1 in the initialization of the sampler, of which the beta distribution approaches the uniform [0,1] distribution whose values can only be between the positive interval 0 to 1. The default posterior mean and standard deviation (sd) were used, along with the median and 95% CI, to explain the variation in soil moisture among treatment types. The comparison of the strength of one treatment over another (P) on soil water levels was performed using the WinBUGS *step( )* function, following the same principal explained for the probability of survival and RHI models.

3.9.4 Chlorophyll Fluorescence (Rank Grass sites only)

It was assumed that the chlorophyll fluorescence data had a normal distribution with only positive values. Therefore, a similar model used to analyzed RHI was fitted to calculate the estimated Y-values of each treatment, and the same Boolean *step ( )* function to determine the strength of one treatment over another in terms of their effects on the observed Y-values.

3.9.5 Carbon Isotope Analysis

It was assumed that the Carbon Isotope signature data had a normal distribution, hence a similar model used to analyzed RHI was fitted to calculate the estimated $\delta^{13}C$ values of each treatment, and the same Boolean *step ( )* function to determine the strength of one treatment over another in terms of their effects on the estimated carbon isotope signature.

The statistical models created for each parameter observed in this research are presented in section 8.1 of the Appendix.

4. Results - Rank Grass Sites

4.1 Tiromoana Bush

4.1.1 Weather data

The monthly averages, standard deviations, maximum and minimum values of the weather data for Tiromoana Bush study site are presented in Table 4-1, referring to 17 months (December-2012 to April-2014) and based on the monthly averages obtained from Waipara West Ews weather station (CliFlo: http://cliflo.niwa.co.nz). The total precipitation (P_{total}) for the 17-month period was 1,086.7 mm, or monthly averages of 63.9 mm. In the 2013 calendar year, precipitation was 809.3 mm or 74.5% of P_{total} for the trial, and higher than the long-term average of 657.8 mm registered by the Waipara West Ews weather station since its establishment in 2007 (https://www.niwa.co.nz). The wettest month of the trial was June-2013 (150.6 mm), and February-2014 was the driest (9.1 mm). Monthly average air temperatures during the experiment ranged between 8.5°C and 19.2°C. The highest maximum air temperature was recorded in January and February-2013 (24°C), and June-2013 experienced the lowest minimum air temperature (Figure 4-1).

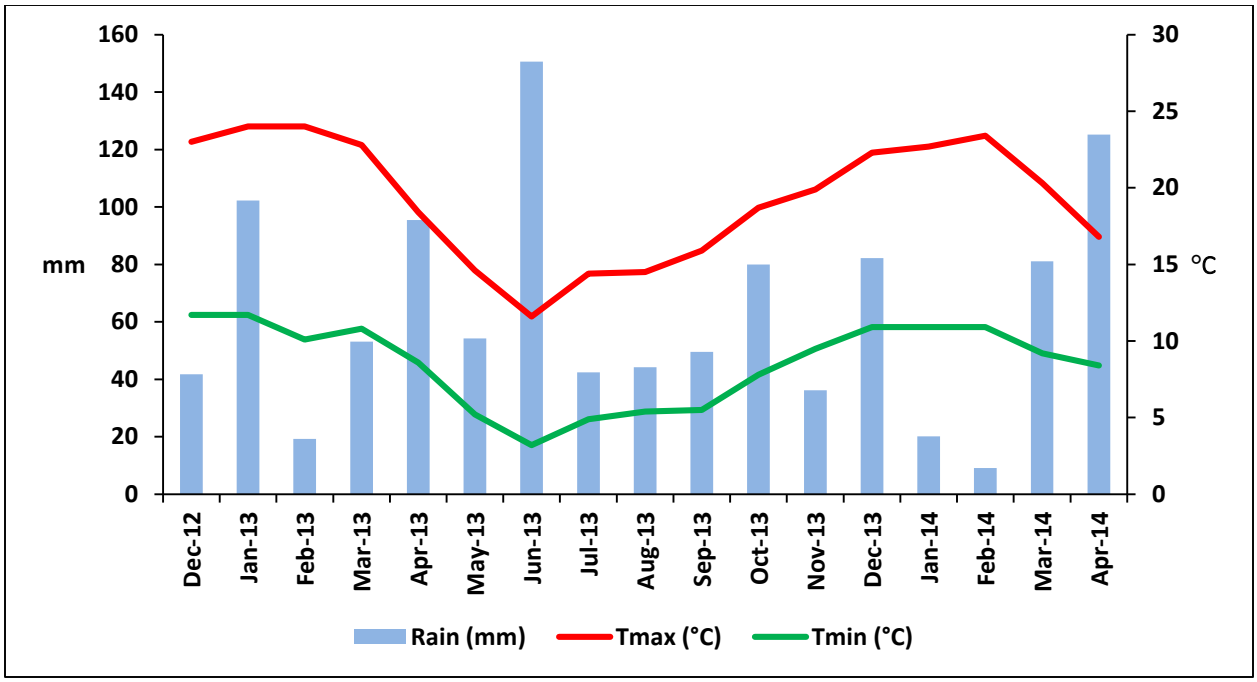


Figure 4-1 Monthly weather averages for Tiromoana Bush for the experimental period. Tmax – maximum air temperature, Tmin – minimum mean temperature. Source: http://cliflo.niwa.co.nz

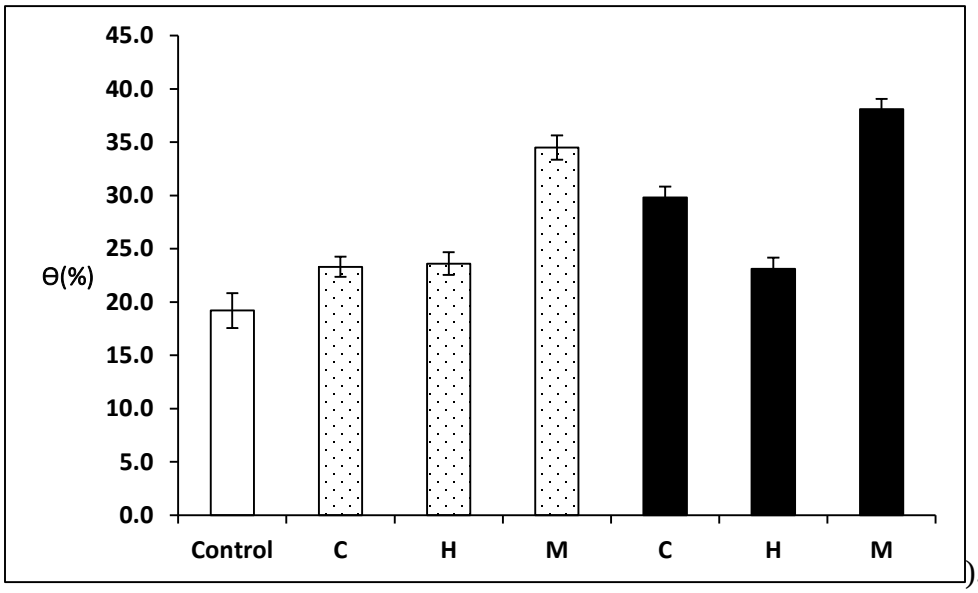
Table 4-1 Weather data summary for the experimental period with averages, standard deviations (sd), maximum and minimum readings for Tiromoana Bush. Tmax – maximum air temperature, Tmin – minimum air temperature. Source: http://www.cliflo.niwa.co.nz

Statistical Parameters	**Rain (mm)**	**Tmax (°C)**	**Tmin (°C)**
Average	63.92	19.2	8.5
sd	37.62	3.9	2.6
Max	150.6	24.0	11.7
Min	9.1	11.6	3.2

4.1.2 Soil-Water Content

Overall, estimated soil water content (Θ%) throughout the experimental period at the Tiromoana Bush study site fluctuated along the seasons (Figure 4-2 A and B), ranging between 25.8% - 40.9% in the first year (December-2012 to October-2013), and from 19.2% to 38.3% in the second year (January and April-2014). The lowest levels tended to be recorded in the control plots, usually between 25.8% and 35.4% in the first year and reaching its lowest average in January-2014 (19.2%). The highest averages were registered in the M+S and M-S treatments (averages ≥ 34%), as well as in most shaded treatments (≥ 35% in the first year and ≥ 22.9% in the second year). Average Θ under all treatments when the trial was established in December-2012 were statistically homogenous (P = 0.41 ~ 0.55), ranging between 33.8% and 36.3%. Planting took place in a dry period (41.8 mm rainfall in December-2012), and nearly half of the total amount of rain in that month (23.0 mm) was recorded in the two weeks that preceded soil moisture monitoring (20/01/2012), with an average maximum air temperature of 29.6°C on that day.

Estimated soil moisture levels in the second summer (January-2014) ranged between 19.2% (control) and 38.1% (M+S) with lower averages (Θ < 25%) in the unshaded plots (except M-S) and in the H+S treatment (



). Soil water content under C+S was 29.8%, and both mulch treatments had averages higher than 30% (M-S = 34.5%, M+S = 38.1%). January-2014 had the lowest monthly precipitation rate and air humidity of the

trial (R = 20.2 mm, RH = 59.5%, respectively, Figure 4-1) and monthly average air temperature of 22.7°C. A total of 7.4 mm of rain was recorded in the two weeks prior to soil-water monitoring, with an estimated maximum air temperature of 22.1°C on the day soil samples were collected (28/01/2014).

Comparisons in Table 4-2 show a marked treatment effect on Θ in January-2014. Θ in the mulched treatments were substantially greater than in the control ($P_{M+S|CONTROL}$ = 0.90, $P_{M-S|CONTROL}$= 0.85). Grass removal method without shade did not produce a statistically greater effect on soil water content compared to the control (P = 0.62 ~ 0.63). Although Θ in the H+S treatment was higher than in the control, differences were not statistically significant (P = 0.62), nor were the differences between H+S and C-S (P = 0.49) or H+S and H-S (P = 0.49). Θ in the C+S was higher than in the control (P = 0.78), C-S (P = 0.72) and H-S treatments (P = 0.71), and also greater than in the H+S (P = 0.72). Estimated Θ in the H-S and C-S was not significantly higher than in the control ($P_{C-S|CONTROL}$ = 0.62, $P_{H-S|CONTROL}$ = 0.63).

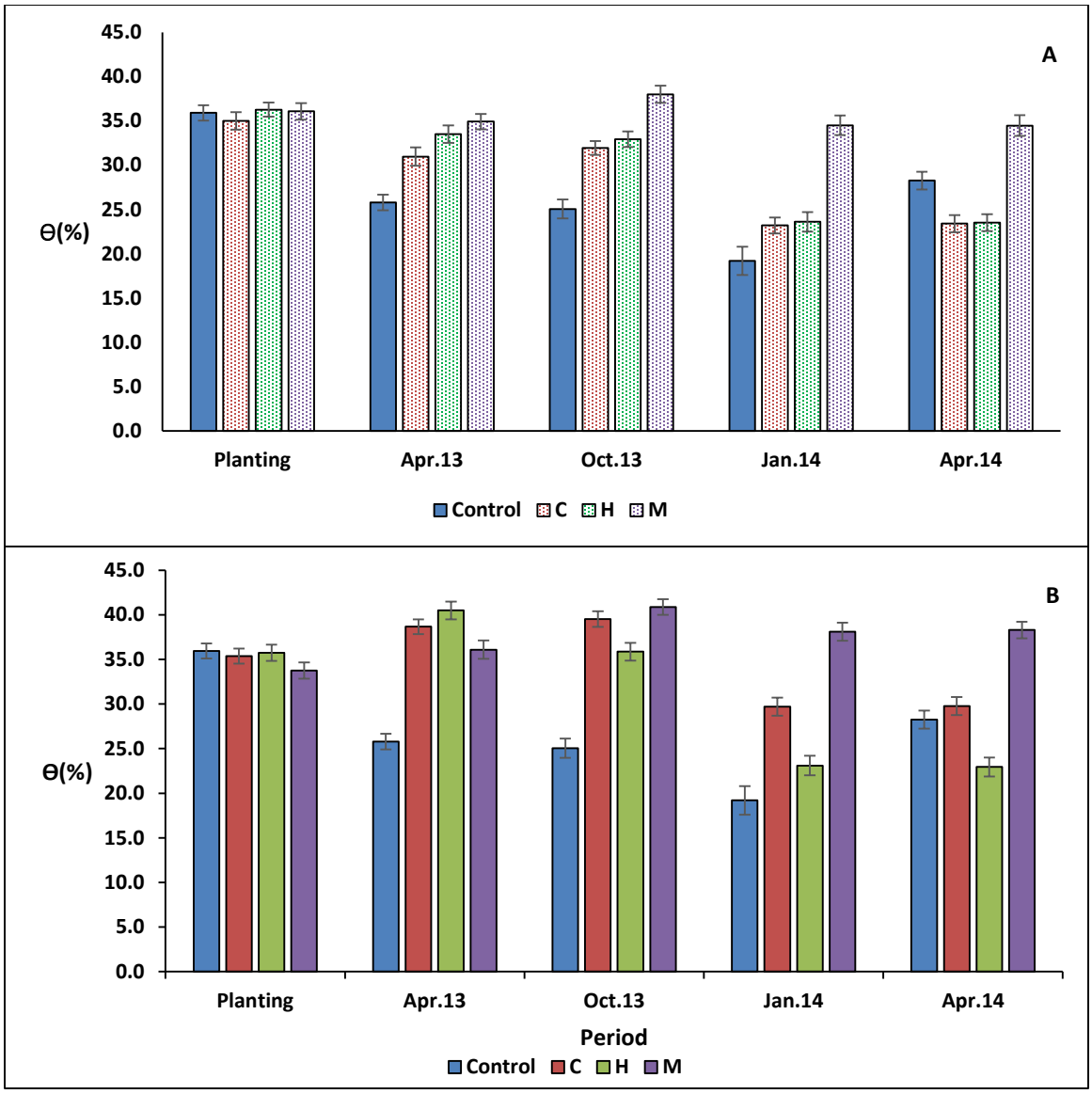


Figure 4-2 Average soil water content and respective 95% credible intervals (CI) per treatment in each monitored period. A - control and grass removal treatments without shade; B - control and grass removal treatments with shade. C – cultivation, H – herbicide, M – mulch Tiromoana Bush.

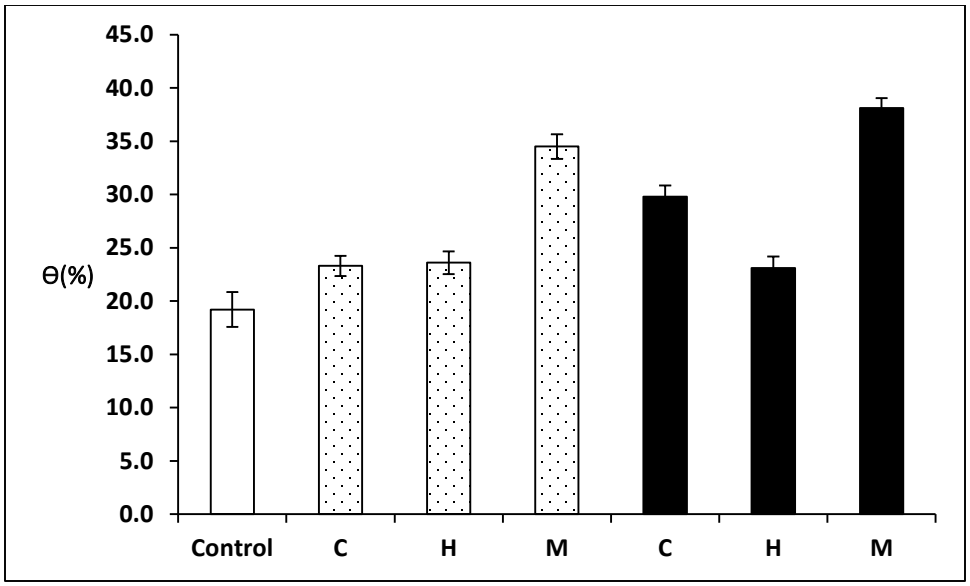


Figure 4-3 Estimated soil water content and respective 95% credible intervals, under each treatment in January-2014. Tiromoana Bush. Pattern fill: grass removal without shade. Solid fill: grass removal with shade. Tiromoana Bush.

Table 4-2 Comparison of estimated soil water content among treatments in January-2014. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., P(ΘA > ΘB|data), where Θ refers to estimated soil water content. Tiromoana Bush.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.62	0					
H-S	0.63	0.51	0				
M-S	0.85	0.83	0.81	0			
C+S	0.78	0.72	0.71	0.35	0		
H+S	0.62	0.49	0.49	0.18	0.28	0	
M+S	0.90	0.88	0.87	0.62	0.76	0.89	0

4.1.3 Survival and Growth

Number of survivors at the end of the experiment in Tiromoana Bush was equal for both species (201 or 79.7%), with the highest number of surviving individuals found in the shaded treatments. *Kunzea robusta* seedlings had the highest number of survivors in the H+S (35), and *Pittosporum tenuifolium* seedlings were in highest numbers in the C+S and M+S treatments, both with 35 individuals. The lowest number of surviving seedlings of both species was found in the M-S: 19 individuals of *K. robusta* and 8 of *P. tenuifolium* (Table 4-3).

Table 4-3 Total number of surviving seedlings per species under each treatment at the end of the experiment: C – cultivation, H – herbicide, M – mulch. Tiromoana Bush.

Treatment	***Kunzea robusta***	***Pittosporum tenuifolium***
Control	23	28
	No shade	
C	34	31
H	25	30
M	19	8
	Shade	
C	31	35
H	35	34
M	34	35
Total	201	201

Kunzea robusta

Kunzea robusta seedlings displayed the highest estimated probability of survival in the shaded treatments (≥ 86%), but also high values in the C-S (0.94) and H-S (0.70) treatments. The lowest probability of survival for *K. robusta* seedlings was in the M-S (0.53) and control treatments (0.64; Figure 4-4A). Comparisons among treatments in Table 4-4 show a strong grass removal and shade effect compared to control ($P \geq 0.97$). Cultivation alone also had a marked effect on

increasing seedling survival compared to control (P = 1.00). Seedlings had higher probability of survival in the H-S than in the control, but differences may be considered statistically weak ($P_{H\text{-}S|CONTROL}$ = 0.69). Probability of survival in the M-S was much lower than in the control in 80% of the simulations.

Figure 4-5 shows that mean heights of *K. robusta* seedlings at the start of the trial varied between 28.2 and 30.7 cm. Mean heights increased under all treatments during the first summer, and ranged from approximately 33.0 cm (control) to 60.3 cm (M+S) in April-2014. Between April and October-2013, mean heights of seedlings continued to grow under most treatments, except in the M-S, where seedlings had dieback instead. Mean heights in October-2013 ranged from 34.9 cm (control) to 67.1 cm (M+S). Mean heights continued to increase in the second summer and, by the end of the experiment, averages ranged from 51.3 cm (control) to 107.5 cm (M+S).

K. robusta seedlings had positive relative height increments (RHI) under all treatments (Figure 4-4B). Seedlings had the highest RHI value in the M+S treatment (1.41) and lowest value in the control plots (0.37). The simulations in Table 4-5 show that seedlings had higher RHI in all treatments than in the control ($P \geq 0.99$). Grass removal methods promoted higher growth increments for *K. robusta* seedlings when combined with shade ($P \geq 0.77$), particularly M+S plots ($P \geq 0.80$). In the absence of shade, C-S was more effective for seedling survival than M-S ($P_{C\text{-}S|M\text{-}S}$ = 0.80) and H-S ($P_{C\text{-}S|H\text{-}S}$ = 0.85), whereas M-S and H-S had statistically similar results ($P_{M\text{-}S|H\text{-}S}$ = 0.51).

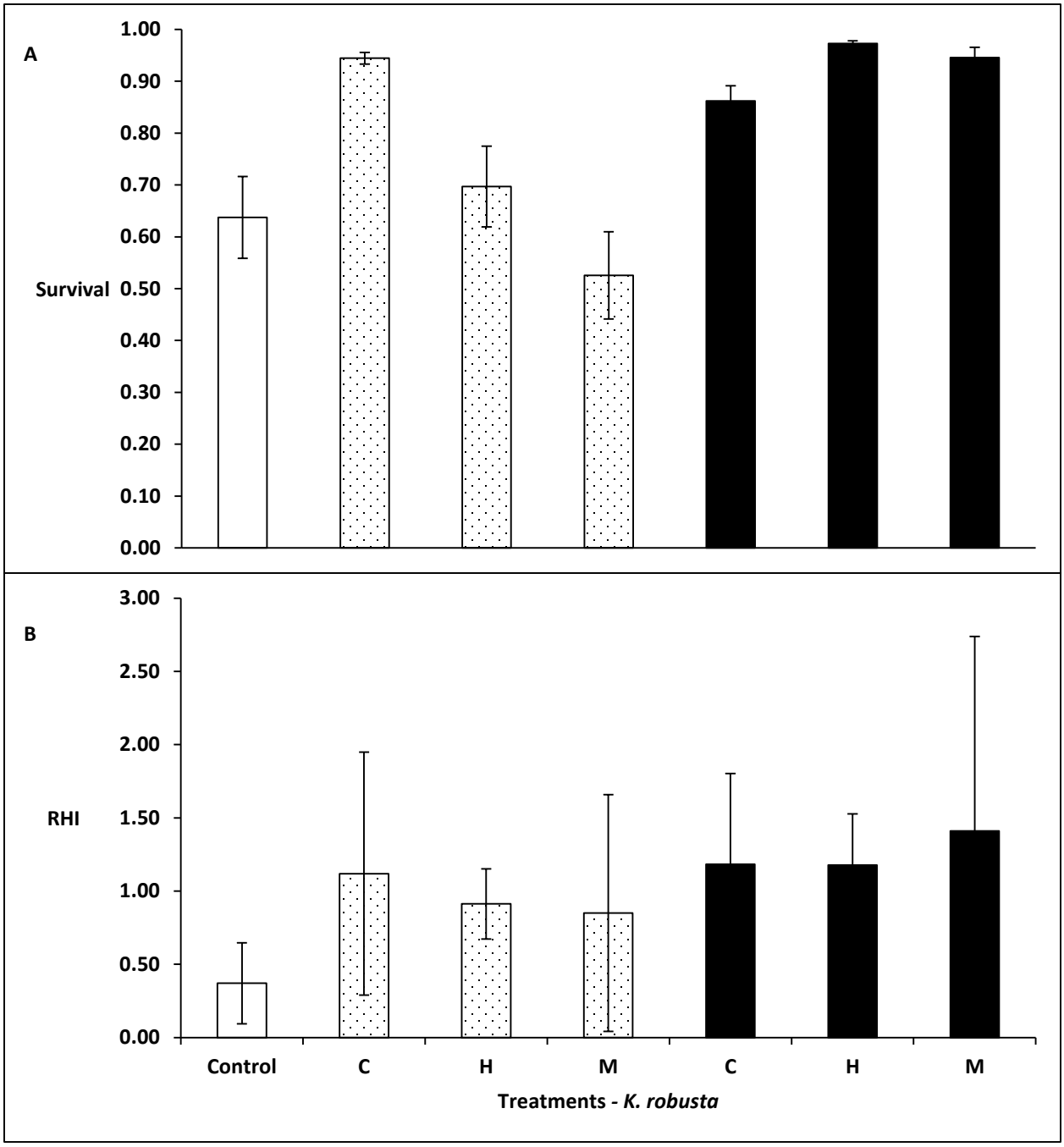


Figure 4-4 Estimated probabilities of survival (A) and Relative Height Increment (B), respective 95% credible intervals, per treatment, for *Kunzea robusta* seedlings. C – cultivation, H – herbicide, M – mulch. Pattern fill: grass removal without shade. Solid fill: grass removal with shade. Tiromoana Bush.

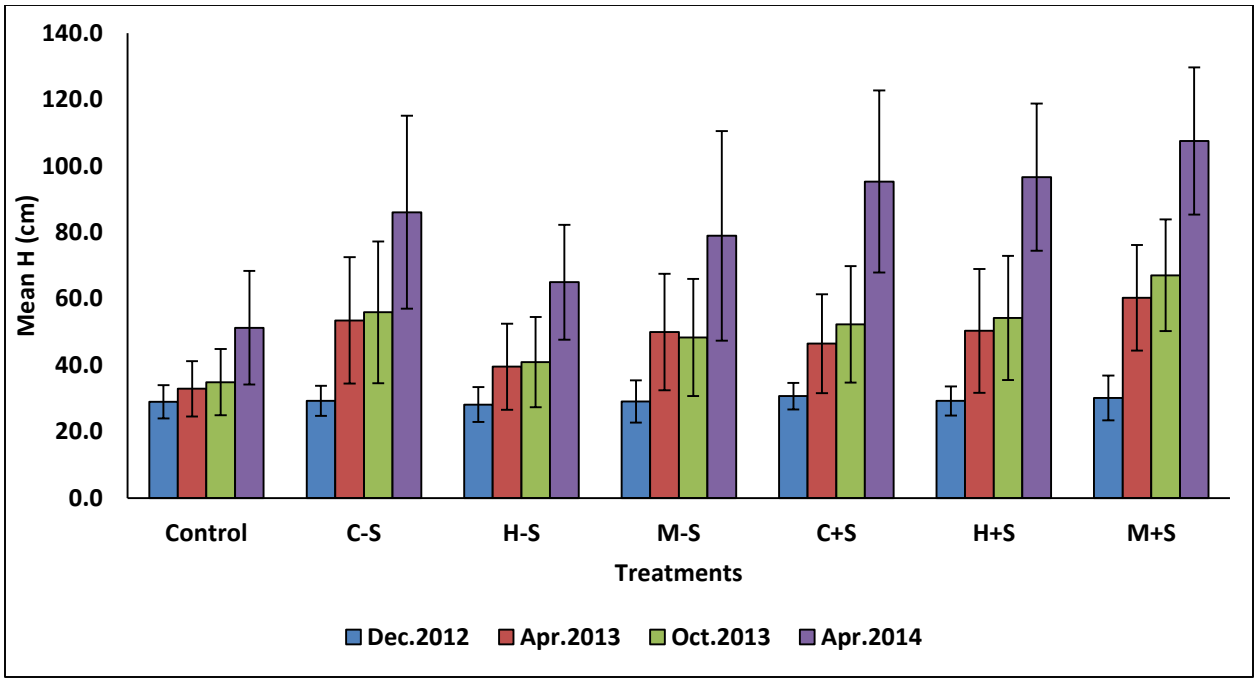


Figure 4-5 Mean heights (cm) of *Kunzea robusta* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. Tiromoana Bush.

Table 4-4 Comparison of probability of survival among treatments for *Kunzea robusta* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(estS_A > estS_B|data)$, where estS refers to estimated probability of survival. Tiromoana Bush.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	1.00	0					
H-S	0.69	0.01	0				
M-S	0.20	0.00	0.09	0			
C+S	0.97	0.11	0.92	1.00	0		
H+S	1.00	0.75	1.00	1.00	0.97	0	
M+S	1.00	0.52	1.00	1.00	0.92	0.28	0

Table 4-5 Comparison of estimated RHI among treatments for *Kunzea robusta*. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(RHI_A > RHI_B|data)$. Tiromoana Bush.

Treatment	Control	C-S	H-S	M-S	C+S	H+S	M+S
Control	0						
C-S	1.00	0					
H-S	0.99	0.15	0				
M-S	0.99	0.20	0.51	0			
C+S	1.00	0.77	0.95	0.93	0		
H+S	0.99	0.87	0.97	0.96	0.64	0	
M+S	1.00	0.98	1.00	0.99	0.89	0.80	0

Pittosporum tenuifolium

Estimated probabilities of survival of *P. tenuifolium* seedlings were ≥ 78% under most treatments, except in M-S (22.2%), where there were only 8 individuals left by the end of the trial (Figure 4-7A). *P. tenuifolium* seedlings had the highest survival in the shaded treatments (≥ 94%). The statistical analyses comparing treatments (Table 4-6) indicate a strong grass removal-and-shade effect on this variable compared to control ($P \geq 0.95$). In the absence of shade, the effects of C-S and H-S on seedling survival were greater than for the control, although differences between these grass-removal-only treatments and control were weak ($P_{C\text{-}S|CONTROL} = 0.68$, $P_{H\text{-}S|CONTROL} = 0.64$). M-S had no beneficial effect on *P. tenuifolium* seedling survival compared to control and to all other treatments ($P_{M\text{-}S} = 0.00$). Comparing grass removal methods in the shaded treatments, probability of survival was higher in the C+S than in the H+S in 76% of the simulations ($P_{C+S|H+S} = 0.76$). M+S also had stronger effect on seedling survival than H+S in 74% of the simulations ($P_{M+S|H+S} = 0.74$). C+S and M+S promoted relatively similar results ($P_{C+S|M+S} = 0.52$), whereas H+S was, statistically, the least effective of the shaded treatments.

Mean heights of *P. tenuifolium* seedlings at the start of the trial ranged from 19.07 to 24.12 cm (Figure 4-6), which more than doubled in the shaded treatments during the first summer, and reached averages ranging from 30.2 cm (control) to 54.7 cm (M+S). Between April and October-2013, mean heights of seedlings continued to increase under most treatments, except in the C-S and M-S treatments. Mean heights in October-2013 ranged from 31.1 cm (control) to 71.3 cm (M+S). Dieback was not recorded in the following growing season, between October-2013 and April-2014, and mean heights by the end of the experiment ranged from 42.4 cm (control) to 94.9 cm (M+S).

The highest RHI values for *P. tenuifolium* seedlings were in the shaded treatments (Figure 4-7B). Comparisons in Table 4-7 show a strong grass removal and shade effect compared to control (P = 1.00), as well as a greater effect of grass removal only on RHI than the control ($P_{C\text{-}S} = 0.81$, $P_{H\text{-}S} = 0.95$, $P_{M\text{-}S} = 1.00$). RHI was larger in the C+S plots in 100% of the simulations compared to control, C-S and H-S, and also higher than in the M-S plots in 81% of the tests. Among the shaded treatments, RHI of seedlings planted in the C+S was higher than in the M+S ($P_{C+S|M+S} = 0.79$). Estimated RHI in the C+S was greater than in the H+S treatment, although differences can be considered statistically small ($P_{C+S|H+S} = 0.67$). In unshaded conditions, *P. tenuifolium* seedlings presented substantially higher RHI values in the M-S than in the C-S ($P_{M\text{-}S|C\text{-}S} = 0.96$), that were also higher than in the H-S treatment ($P_{M\text{-}S|H\text{-}S} = 0.91$). In contrast, C-S promoted the lowest estimated growth rates compared to the other grass removal methods ($P_{C\text{-}S} \leq 0.21$).

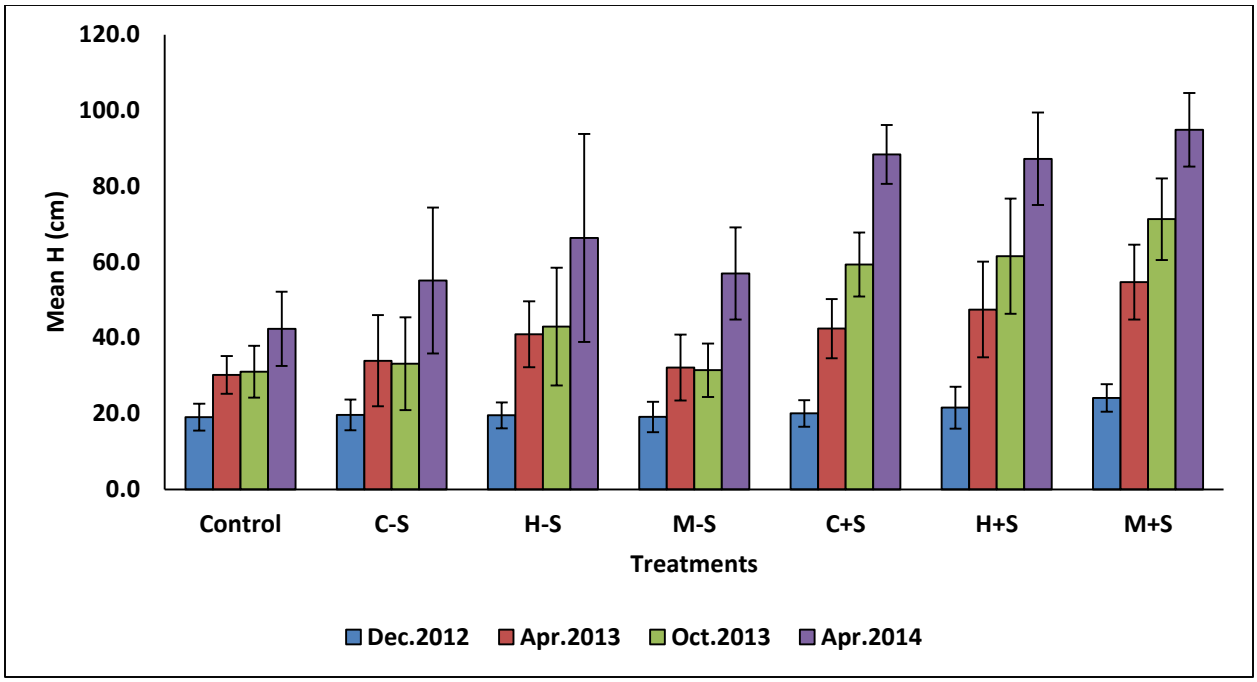


Figure 4-6 Mean heights (cm) of *Pittosporum tenuifolium* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. Tiromoana Bush.

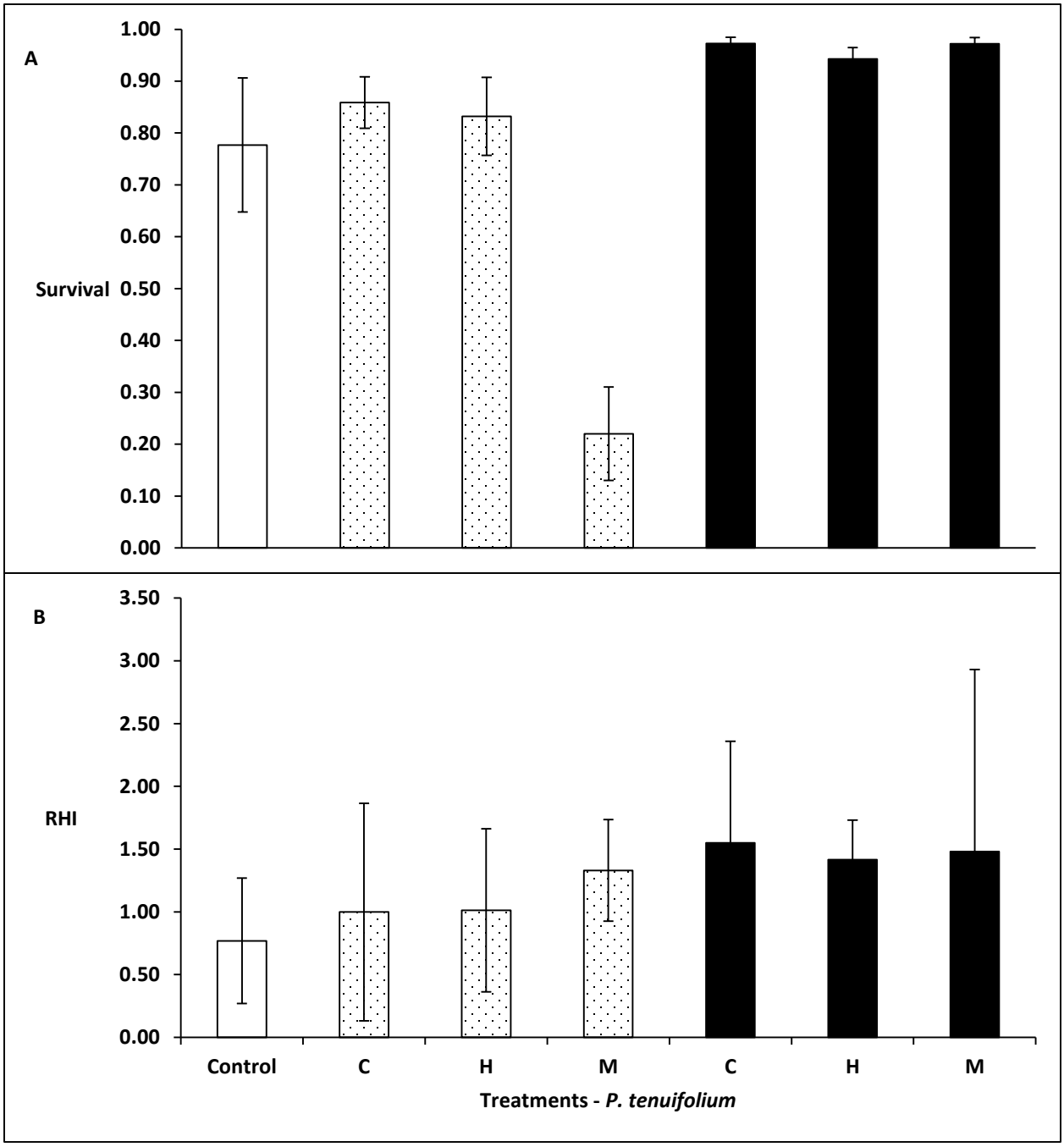


Figure 4-7 Estimated probabilities of survival (A) and Relative Height Increment (B), respective 95% credible intervals, per treatment, for *Pittosporum tenuifolium* seedlings. C – cultivation, H – herbicide, M – mulch. Pattern fill: grass removal without shade. Solid fill: grass removal with shade. Tiromoana Bush.

Table 4-6 Comparison of estimated probability of survival among treatments for *Pittosporum tenuifolium* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., P($estS_A$ > $estS_B$|data), where estS refers to estimated probability of survival. Tiromoana Bush.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.68	0					
H-S	0.64	0.45	0				
M-S	0.00	0.00	0.00	0			
C+S	0.98	0.96	0.97	1.00	0		
H+S	0.95	0.85	0.89	1.00	0.24	0	
M+S	0.98	0.96	0.96	1.00	0.48	0.74	0

Table 4-7 Comparison of estimated RHI among treatments for *Pittosporum tenuifolium*. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., P(RHI_A > RHI_B|data). Tiromoana Bush.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.81	0					
H-S	0.95	0.79	0				
M-S	1.00	0.96	0.91	0			
C+S	1.00	1.00	1.00	0.81	0		
H+S	1.00	0.99	0.99	0.71	0.33	0	
M+S	1.00	1.00	0.99	0.60	0.21	0.36	0

4.1.4 Chlorophyll Fluorescence

Chlorophyll fluorescence readings (Y-values) of both *Kunzea robusta* and *Pittosporum tenuifolium* seedlings fluctuated throughout the trial, with peak averages in mid-summer (January-2014) and lowest Y-values in spring (November-2013). Estimated Y-values were ≥ 777.4 for *K. robusta* seedlings and ≥ 738.3 for *P. tenuifolium* seedlings over the entire experimental period. Average Y-values of *K. robusta* and *P. tenuifolium* seedlings were higher in the second summer than in the first (Figure 4-8).

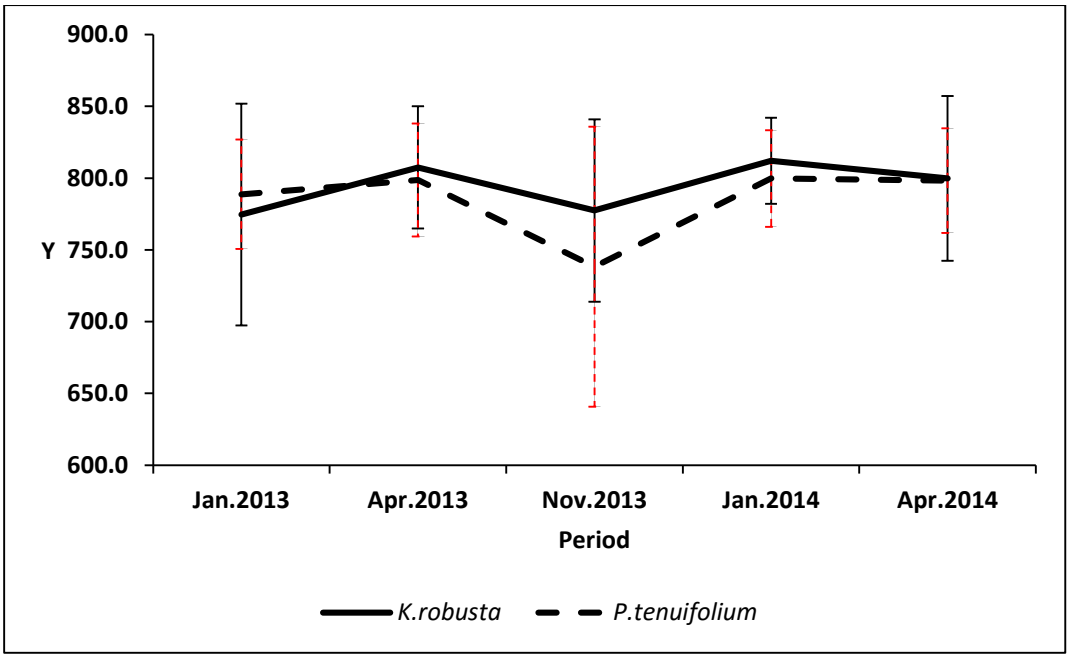


Figure 4-8 Average Y-values and respective 95% credible intervals of *Kunzea robusta* and *Pittosporum tenuifolium* seedlings throughout the experiment period. Tiromoana Bush.

Kunzea robusta

In January-2014, estimated Y-values were ≥ 780.6 (Figure 4-9) and markedly higher in the shaded treatments compared to control plots (P = 0.75 ~ 0.76), and also higher than in the unshaded treatments (P ≥ 0.61), though differences were statistically small. Estimated Y-values of *K. robusta* seedlings were significantly higher in the M+S than in the M-S ($P_{M+S|M-S}$ = 0.88) and more elevated in the C+S than in the C-S ($P_{C+S|C-S}$ = 0.73) treatments. Although average Y-

values in the H+S were more elevated than in the H-S, differences between these treatments can be considered irrelevant ($P_{H+S|H-S}$ = 0.64). Seedlings presented markedly higher estimated Y-values in the H+S compared to C-S ($P_{H+S|C-S}$ = 0.76) and to M-S ($P_{H+S|M-S}$ = 0.88). Estimated Y-values in the M-S were lower than in all other treatments in over 70% of the simulations. As for C-S and H-S, differences in estimated Y-values were statistically small ($P_{C-S|H-S}$ = 0.60), as were the differences between these two treatments and control ($P_{C-S|CONTROL}$ = 0.51, $P_{H-S|CONTROL}$ = 0.62, Table 4-8).

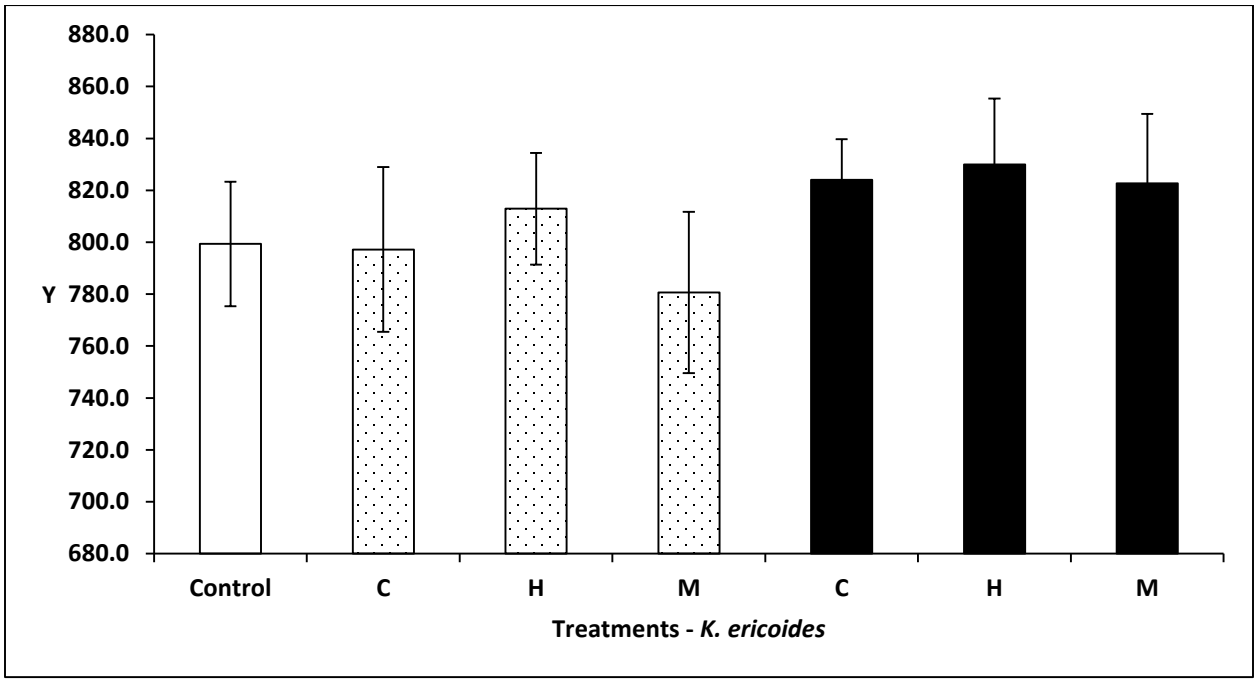


Figure 4-9 Estimated chlorophyll fluorescence readings and respective 95% credible intervals, per treatment, for *Kunzea robusta* seedlings per treatment in January-2014. Pattern fill – grass removal and no-shade treatments. Solid fill – grass removal and shade treatments. Tiromoana Bush.

Table 4-8 Comparison of estimated Y-values among treatments in January-2014 for *Kunzea robusta* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(Y_A > Y_B|data)$, where Y refers to estimated chlorophyll fluorescence. Tiromoana Bush.

Treatment	Control	C-S	H-S	M-S	C+S	H+S	M+S
Control	0						
C-S	0.51	0					
H-S	0.62	0.60	0				
M-S	0.30	0.27	0.20	0			
C+S	0.75	0.73	0.61	0.89	0		
H+S	0.75	0.76	0.64	0.88	0.51	0	
M+S	0.76	0.73	0.62	0.88	0.51	0.47	0

Pittosporum tenuifolium

P. tenuifolium seedlings had estimated Y-values ≥ 778.1 in January-2014 (Figure 4-10), with higher averages in the shaded treatments than in the control in more than 70% of the simulations (Table 4-9). Grass removal in the absence of shade, on the other hand, did not have a strong effect on this parameter compared to control (P = 0.40 ~ 0.57). Seedlings in the H+S had markedly higher estimated Y-values than in the H-S ($P_{H+S|H-S}$ = 0.83). Averages were also higher in the M+S than in the M-S ($P_{M+S|M-S}$ = 0.75). Estimated Y-values in the C+S were considerably higher than in the H-S and M-S ($P_{C+S|H-S}$ = 0.78, $P_{C+S|M-S}$ = 0.74). Although averages in the C+S were higher than in the C-S, the difference may be considered statistically small ($P_{C+S|C-S}$ = 0.60). The same can be said for the comparisons between M+S and H+S compared to C-S ($P_{M+S|C-S}$ = 0.63, $P_{H+S|C-S}$ = 0.68).

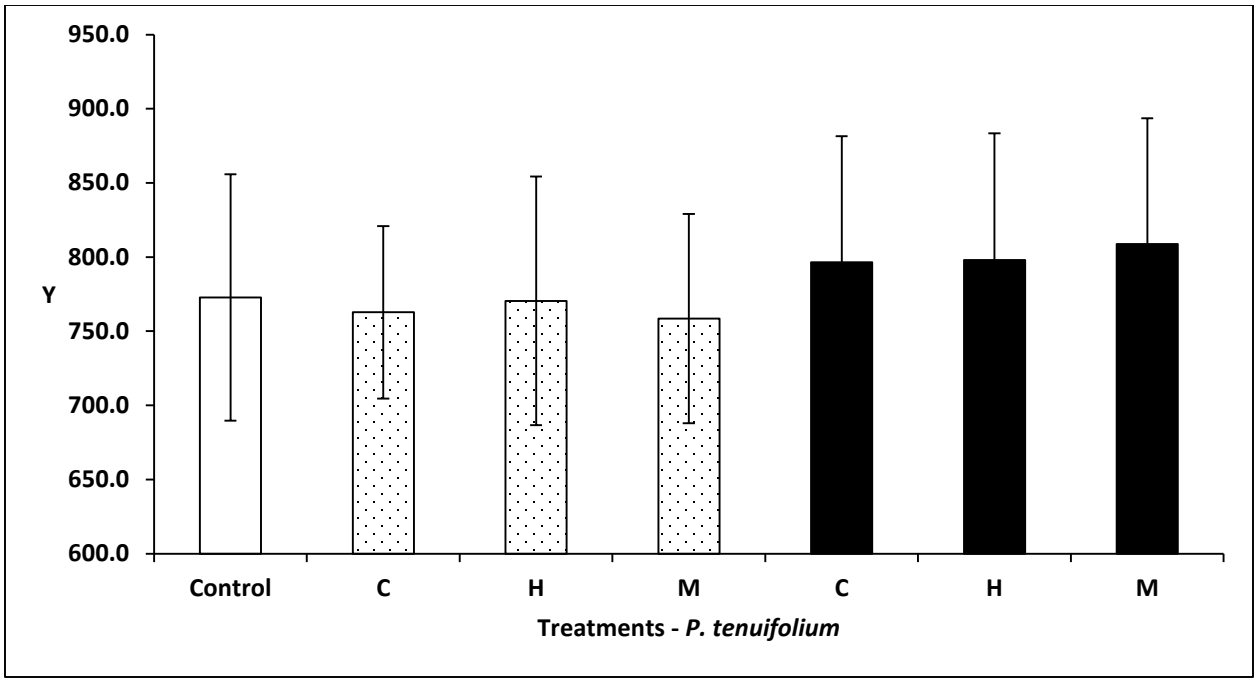


Figure 4-10 Estimated Y-values and respective 95% credible intervals, per treatment, for *Pittosporum tenuifolium* seedlings in January-2014. Patter fill – grass removal and no-shade treatments. Solid fill – grass removal and shade treatments. Tiromoana Bush.

Table 4-9 Comparison of estimated chlorophyll fluorescence readings among treatments in January-2014 for *Pittosporum tenuifolium* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(Y_A > Y_B|data)$, where Y refers to estimated chlorophyll fluorescence. Tiromoana Bush.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.57	0					
H-S	0.40	0.34	0				
M-S	0.42	0.37	0.49	0			
C+S	0.71	0.60	0.78	0.74	0		
H+S	0.76	0.68	0.83	0.78	0.57	0	
M+S	0.70	0.63	0.80	0.75	0.52	0.46	0

4.1.5 Carbon Isotope Analysis - $\delta^{13}C$

Estimated $\delta^{13}C$ values of *K. robusta* seedlings varied from -28.98‰ to -31.36‰ (Figure 4-11), and tended to be lower (more negative) in most shaded treatments than unshaded and control plots (Table 4-10), although averages were lower in the H+S compared to control ($P_{H+S|control}$ = 0.43). Estimated $\delta^{13}C$ values in the shaded were more negative than in the M-S ($P \leq 0.69$), and seedlings in the M-S also had lower averages than in the other unshaded treatments ($P \leq 0.43$). However, differences among all treatments were not statistically significant ($P = 0.34 \sim 0.69$). Estimated $\delta^{13}C$ values of *P. tenuifolium* seedlings varied from -27.90‰ to -29.52‰ (Figure 4-12), and tended to be more negative in the shaded treatments (Figure 4-12). Estimated $\delta^{13}C$ values varied among treatments and were generally lower in the shaded than in the control treatments ($P = 0.51 \sim 0.55$); however, differences among all treatments may be considered statistically irrelevant ($P = 0.42 \sim 0.63$, Table 4-11).

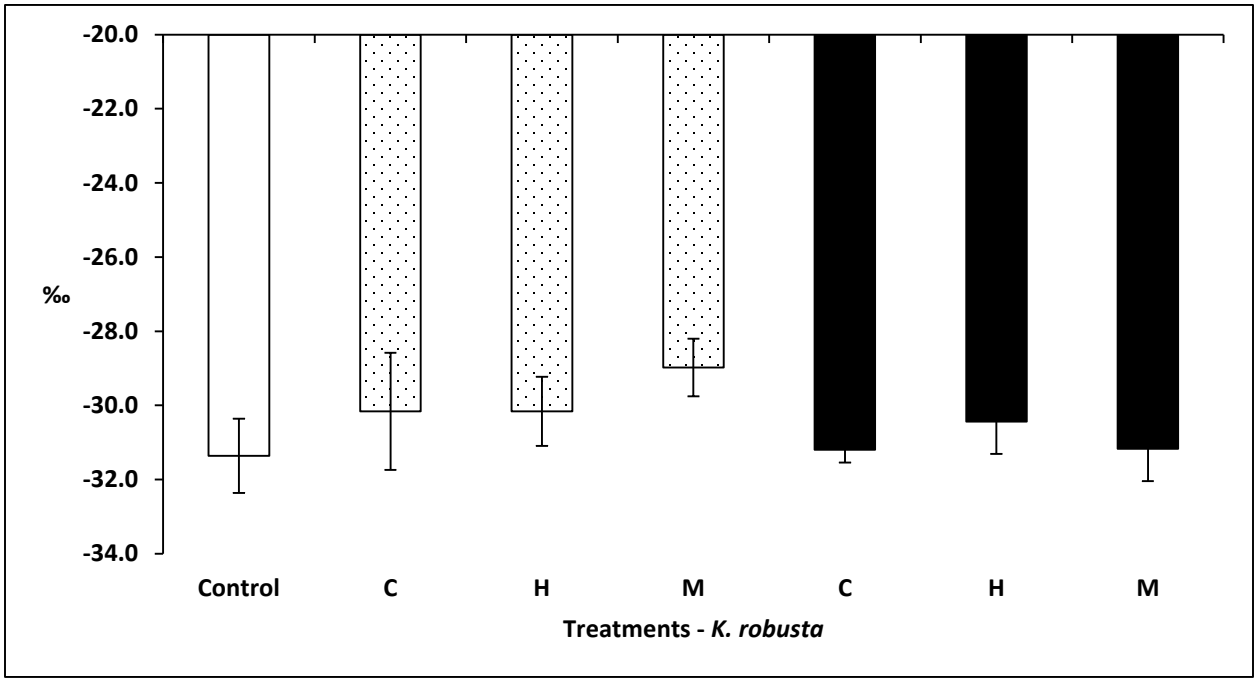


Figure 4-11 Estimated $\delta^{13}C$ values and respective 95% credible intervals, per treatment, for *Kunzea robusta* seedlings per treatment. Tiromoana Bush.

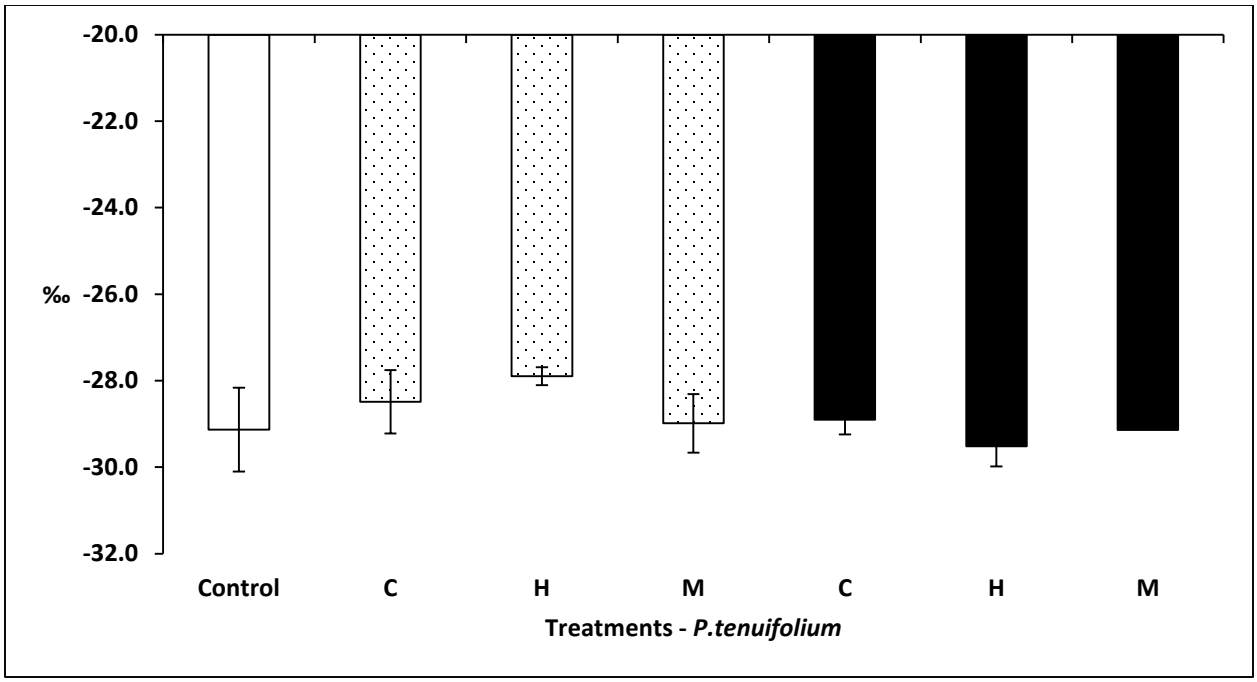


Figure 4-12 Estimated $\delta^{13}C$ values and respective 95% credible intervals of *Pittosporum tenuifolium* seedlings, per treatment. Tiromoana Bush.

Table 4-10 Comparison of $\delta^{13}C$ values among treatments for *Kunzea robusta* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\delta_A > \delta_B|data)$, where δ refers to estimated $\delta^{13}C$ values. Tiromoana Bush.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.41	0					
H-S	0.44	0.52	0				
M-S	0.34	0.43	0.39	0			
C+S	0.54	0.62	0.59	0.69	0		
H+S	0.43	0.55	0.50	0.61	0.43	0	
M+S	0.50	0.59	0.57	0.66	0.47	0.55	0

Table 4-11 Comparison of $\delta^{13}C$ values among treatments of *Pittosporum tenuifolium* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\delta_A > \delta_B|\text{data})$, where δ refers to estimated $\delta^{13}C$ values. Tiromoana Bush.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.45	0					
H-S	0.42	0.47	0				
M-S	0.50	0.54	0.59	0			
C+S	0.55	0.59	0.61	0.50	0		
H+S	0.53	0.60	0.63	0.55	0.54	0	
M+S	0.51	0.56	0.59	0.49	0.48	0.47	0

4.2 Willows Reserve

4.2.1 Weather Data

The total precipitation rate (P_{total}) for the period of the trial (17 months) was 1,070 mm, and an average of 60.3 mm/month, mostly concentrated in autumn and spring (Table 4-12). In the 2013 calendar year, the amount of precipitation was 682.8 mm or 63.8% of P_{total}, and higher than the long-term average of 609.5 mm between 1994 and 2013 obtained from the Christchurch Airport weather station (https://www.niwa.co.nz). The highest precipitation level recorded was in June-2013 (186.8 mm), and the lowest monthly average was 12.2 mm in January-2014. Average monthly maximum air temperature was 18.4°C, with highest averages in January-2013 (23.9°C) and lowest temperatures in July-2013 (1.5°C, Figure 4-13).

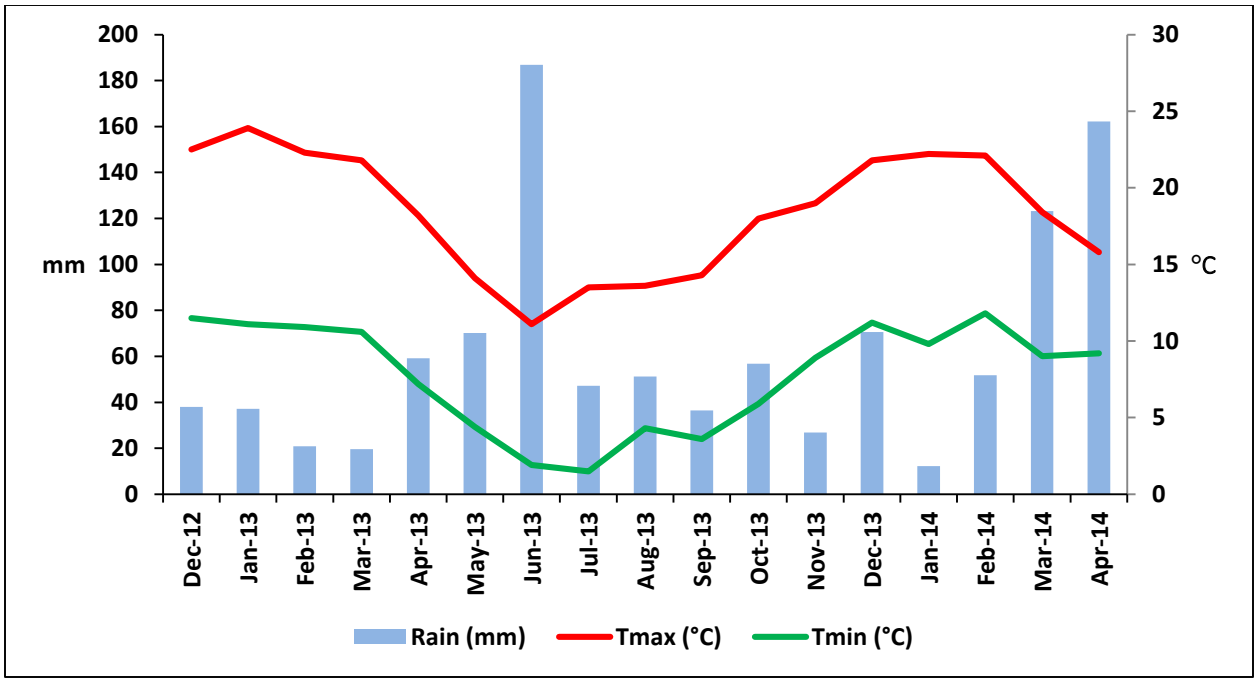


Figure 4-13 Monthly weather averages for The Willows Reserve for the experimental period. Tmax – maximum air temperature, Tmin – minimum air temperature. Source: www.cliflo.niwa.co.nz.

Table 4-12 Weather data summary for the experimental period with averages, standard deviations (sd), maximum and minimum readings for The Willows Reserve. Tmax – maximum air temperature, Tmin – minimum air temperature. Source: www.cliflo.niwa.co.nz.

Statistical Parameters	**Rain (mm)**	**Tmax (°C)**	**Tmin (°C)**
Average	62.95	18.4	7.8
sd	47.91	3.9	34
Max	186.8	23.9	11.8
Min	12.2	11.1	1.5

4.2.2 Soil Water Content

Estimated soil water content (Θ) at the Willows Reserve study site fluctuated across seasons during the experimental period. Estimated Θ was < 30% under all treatments during the entire experimental period, and shaded treatments mostly had higher estimated Θ than unshaded treatments and the control plots (Figure 4-14). Averages at planting in December-2012 were ≤ 20% and relatively homogenous under all treatments around the site ($P = 0.40 \sim 0.77$). The average monthly air temperature in December-2012 was 22.5°C, and monthly precipitation was 38.0 mm (Figure 4-13). A total of 27.2 mm of rain was recorded in the two weeks that preceded planting, most of it on one day (25.8 mm on 7/12/2012), ten days prior to soil sampling. Average monthly air humidity was 70.2%, the second lowest recorded during the trial, and 11.6% lower than the overall monthly average for the entire experimental period (81.8%, Table 4-12). Maximum air temperature on the day soil samples were collected was the highest of the month (31.2°C) with virtually no rainfall.

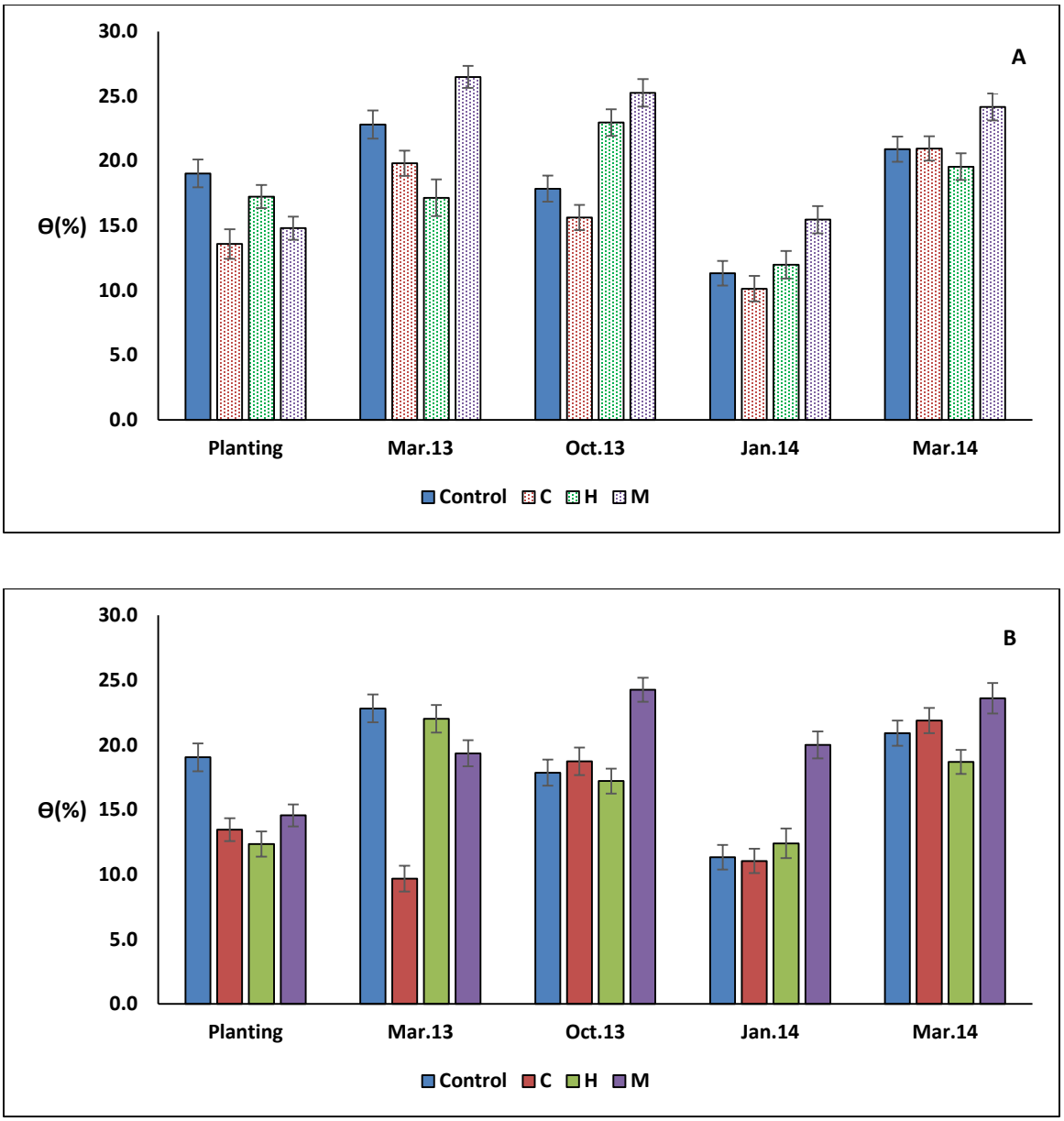


Figure 4-14 Average soil water content and respective 95% credible intervals per treatment in each monitored period. A - control and grass removal treatments without shade; B - control and grass removal treatments with shade. C – cultivation, H – herbicide, M – mulch. Willows Reserve.

Estimated Θ in January-2014 was the lowest recorded in the trial for most treatments, ranging from 10.1% in the C-S to 19.9% in the M+S treatments (Figure 4-15). Monthly average rainfall in January-2014 was 12.2 mm, the lowest monthly total recorded for the experimental period. A total of 7.0 mm of rain was registered two days preceding soil sampling, or 57.4% of the total amount of rain in that month. The average maximum air temperature on the day of soil moisture monitoring (25.5°C) was higher than the monthly average (22.2°C). Relative air humidity was only slightly lower than in December-2012 ($RH_{Jan.14}$ = 65.1%, $RH_{Dec.12}$ = 65.4%), making it the lowest monthly average registered in the entire experimental period (Table 4-12).

The statistical analyses in Table 4-13 indicate that estimated Θ levels in January-2014 were markedly higher in the M+S than in the control (P = 0.83) and considerably more elevated in the M-S compared to control (P = 0.69). Θ levels in the M+S were also distinctly higher than in the C-S and H-S treatments ($P \geq 0.80$), as well as higher than in the C+S (P = 0.85) and H+S plots (P = 0.78). Θ levels in the M-S were markedly more elevated than in the C-S (P = 0.74), and C+S (P = 0.72), but not considerably higher than in the H-S (P = 0.65) and H+S treatments (P = 0.62). Differences in Θ levels between M+S and M-S were also small, though more elevated in the former ($P_{M+S|M-S}$ = 0.69). As for the other treatments (C-S, H-S, C+S, and H+S) in relation to the control, differences in Θ may be considered statistically irrelevant (P = 0.45 ~ 0.56).

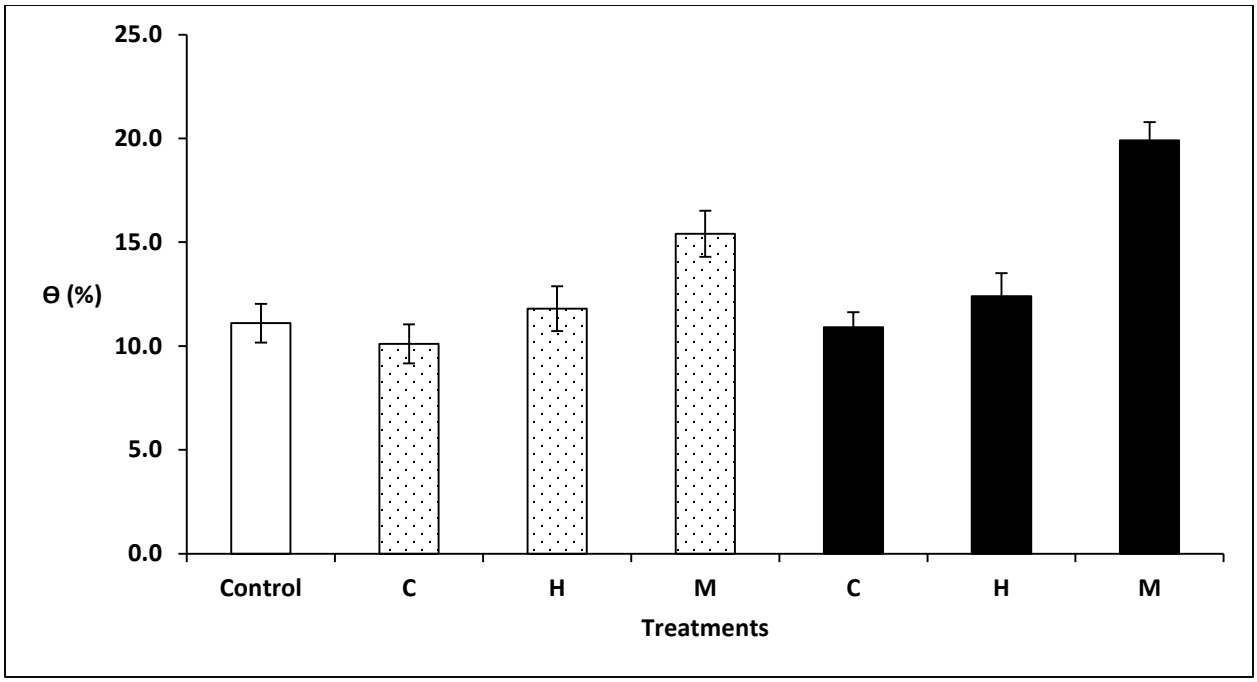


Figure 4-15 Estimated soil water content and respective 95% credible intervals under each treatment in January-2014: Pattern fill – grass removal and no-shade treatments. Solid fill – grass removal and shade treatments. Willows Reserve.

Table 4-13 Comparison of estimated soil water content among treatments (P) in January-2014. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\Theta_A > \Theta_B|\text{data})$, where Θ refers to estimated soil water content. Willows Reserve.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.45	0					
H-S	0.54	0.58	0				
M-S	0.69	0.74	0.65	0			
C+S	0.49	0.53	0.46	0.28	0		
H+S	0.56	0.61	0.54	0.38	0.57	0	
M+S	0.83	0.87	0.80	0.69	0.85	0.78	0

4.2.3 Survival and Growth

A total of 152 seedlings of *Kunzea robusta* (60.3%) and 139 seedlings of *Pittosporum tenuifolium* (55.1%) remained at the end of the experiment (Table 4-14). Seedlings of both species had highest survival rates under the shaded treatments, whilst control and M-S had lowest seedling survivorship. Both species also had highest establishment in the C+S treatment (36/36 *Kunzea robusta* and 35/36 *Pittosporum tenuifolium* seedlings).

Table 4-14 Number of survivors of *Kunzea robusta* and *Pittosporum tenuifolium* seedlings at the end of the experiment (April-2014). Willows Reserve.

Treatment	***Kunzea robusta***	***Pittosporum tenuifolium***
Control	1	1
	No shade	
C	23	24
H	13	12
M	13	5
	Shade	
C	36	35
H	34	33
M	33	29
Total	152	139

Kunzea robusta

Estimated probability of survival of *Kunzea robusta* seedlings was higher under the shaded treatments (≥ 0.94), and ≤ 0.68 in the unshaded and control treatments (Figure 4-16A). Highest probability of seedling survival was recorded in the C+S (1.00). In the absence of shade, *K. robusta* seedlings had higher probabilities in the C-S than in the other unshaded treatments (0.68). Probability of survival was lowest in the H-S (0.29) and control (0.02) plots. Simulation results presented in

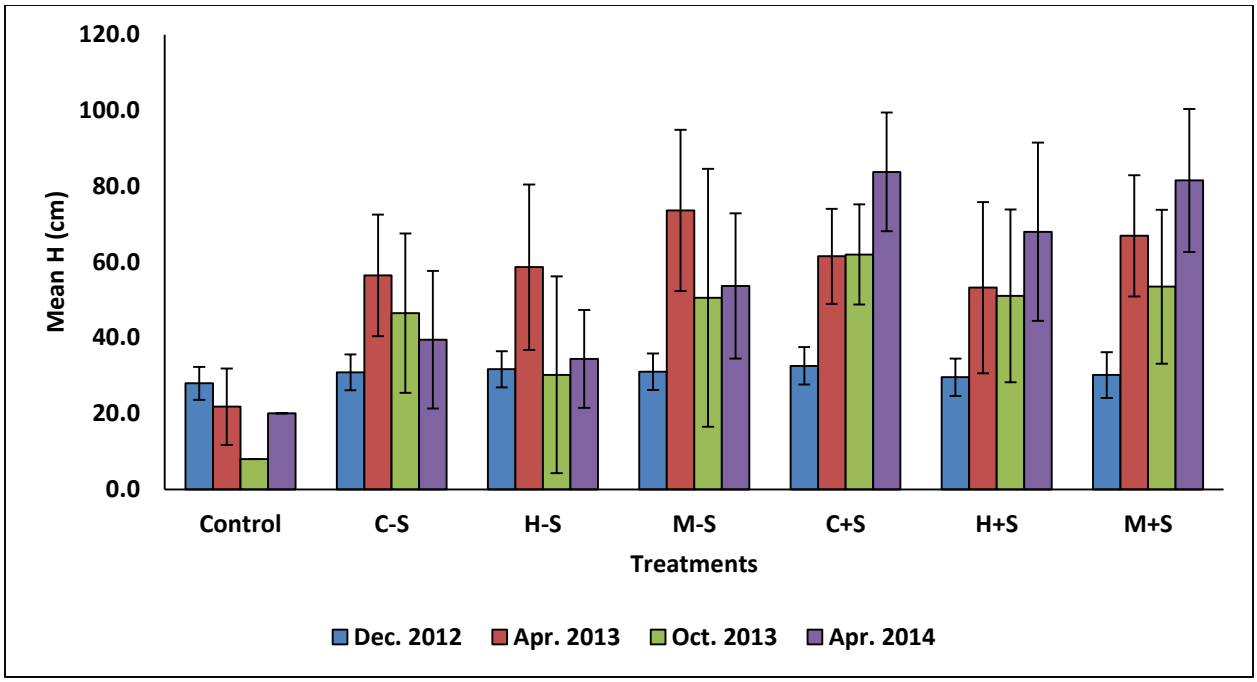


Figure 4-17 Mean heights (cm) of *Kunzea robusta* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. The Willows Reserve.

Table 4-15 show that probability of survival for *K. robusta* seedlings was markedly higher in the shaded treatments compared to control (P = 1.00) and also more elevated than in the unshaded treatments (P ≥ 0.96). C+S was the treatment that resulted in the highest probability of survival for this species (P = 1.00), followed by H+S (P ≥ 0.98) and M+S (P ≥ 0.96). *K. robusta* seedlings had low survival values in the grass-removal-only treatments, though the probabilities in the C-S were expressively higher than in the control ($P_{C\text{-}S|control}$ = 1.00), H-S ($P_{C\text{-}S|H\text{-}S}$ = 0.95), and M-S ($P_{C\text{-}S|M\text{-}S}$ = 0.94).

At planting, *K. robusta* seedlings had mean heights varying from 28.0 cm to 32.6 cm (Figure 4-17), that more than doubled by the next measurement period in April-2013 in the M+S (on average, from 30.2 cm to 66.9 cm) and M-S (on average, from 31.1 cm to 73.6 cm) treatments. Seedlings in the remaining treatments (except control) also increased in mean height between December-2012 and April-2013. Seedlings in the control plots had dieback in the first summer, decreasing in mean height from 28.0 to 21.9 cm, on average. Dieback was recorded for seedlings in all treatments between April and October-2013. Mean heights in October-2013 ranged from

8.0 cm (control) to 62.0 cm (C+S). Growth resumed in the following season, and mean heights of *K. robusta* seedlings were between 20.1 cm and 83.8 cm by the end of the experiment.

K. robusta seedlings had positive RHI values under the shaded, C-S, and H-S treatments, whereas control and H-S plots presented dieback (Figure 4-16B). Simulations comparing estimated RHI between treatments (Table 4-16) show that *K. robusta* seedlings grew markedly more in the shaded treatments than in the control ($P \geq 0.98$). Growth was also higher in the shaded compared to the unshaded treatments ($P \geq 0.88$). Treatments M+S and C+S had relatively similar effects on *K. robusta* seedling growth ($P_{M+S|C+S} = 0.56$), and were both more effective on this parameter than H+S ($P_{M+S|H+S} = 0.88$, $P_{C+S|H+S} = 0.84$). *K. robusta* seedlings had poor development in the absence of shade. Nevertheless, mulch and cultivation had stronger effects on growth than no treatment at all ($P_{M-S|control} = 0.93$, $P_{C-S|control} = 0.81$). Seedlings also had higher RHI in the H-S plots, even though differences between this treatment and control may be considered statistically irrelevant ($P_{H-S|control} = 0.62$).

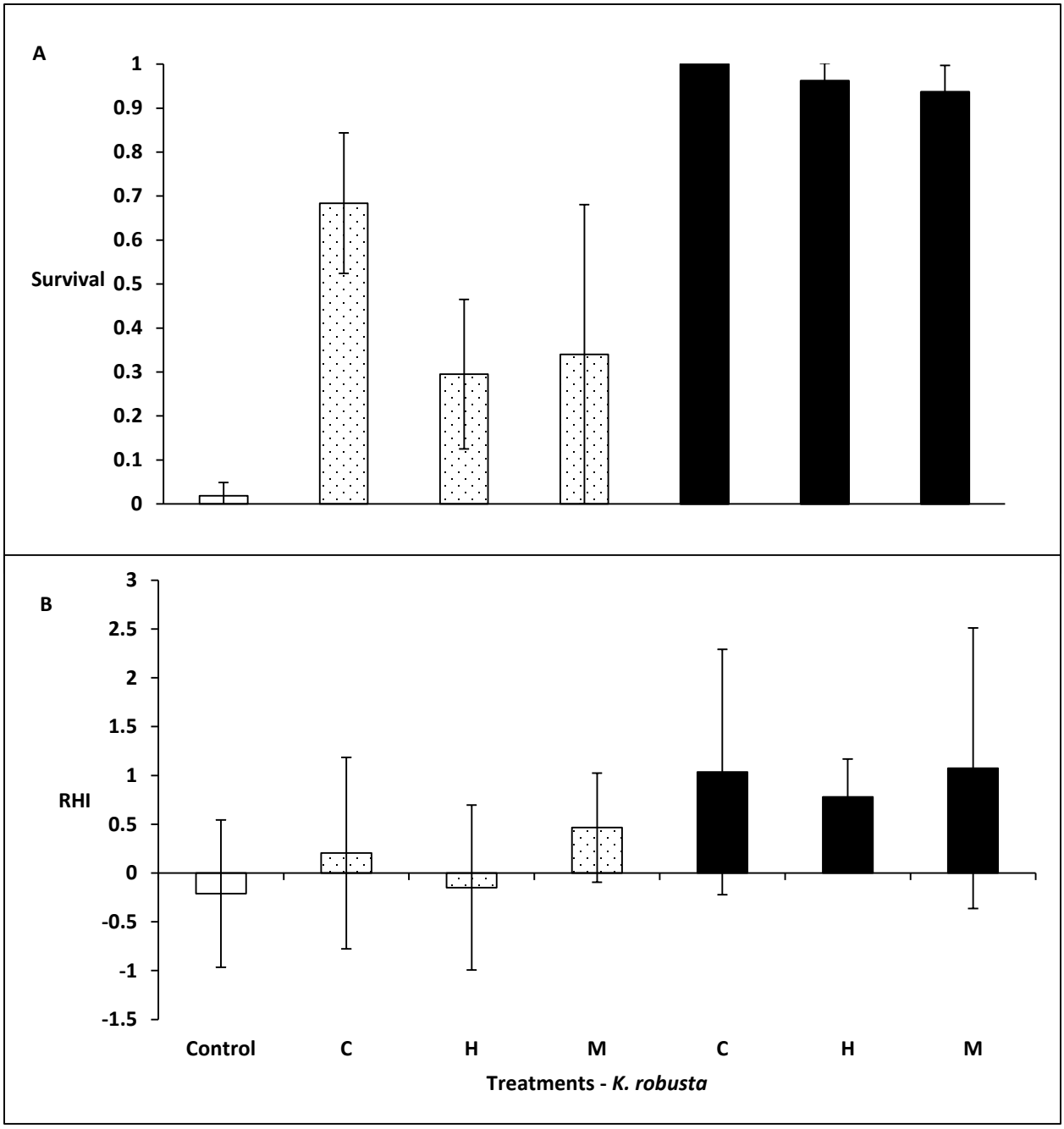


Figure 4-16 Estimated probability of survival (A) and Relative Height Increment (B), and respective 95% credible intervals, for *Kunzea robusta* seedlings, per treatment. Pattern fill – grass removal and no shade treatments. Solid fill – grass removal and shade treatments. C – cultivation, H – herbicide, M – mulch. Willows Reserve.

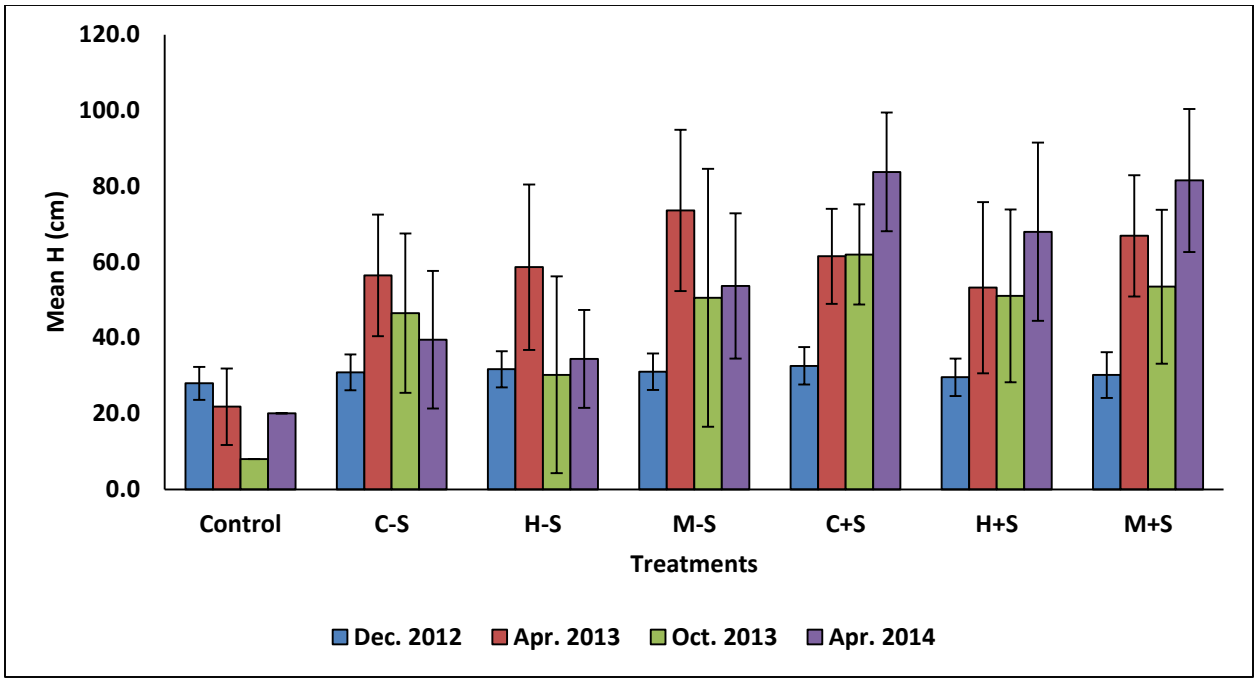


Figure 4-17 Mean heights (cm) of *Kunzea robusta* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. The Willows Reserve.

Table 4-15 Comparison of estimated probability of survival for *Kunzea robusta* among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(estS_A > estS_B|data)$, where estS refers to estimated probability of survival. Willows Reserve.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	1.00	0					
H-S	0.99	0.05	0				
M-S	1.00	0.06	0.58	0			
C+S	1.00	1.00	1.00	1.00	0		
H+S	1.00	0.98	1.00	1.00	0.00	0	
M+S	1.00	0.96	1.00	1.00	0.00	0.34	0

Table 4-16 Comparison of estimated RHI of *Kunzea robusta* seedlings among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(RHI_A > RHI_B|data)$. Willows Reserve.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.81	0					
H-S	0.62	0.17	0				
M-S	0.93	0.94	0.99	0			
C+S	0.99	1.00	1.00	0.97	0		
H+S	0.98	1.00	1.00	0.88	0.17	0	
M+S	0.99	1.00	1.00	0.98	0.56	0.88	0

Pittosporum tenuifolium

Estimated probability of survival of *Pittosporum tenuifolium* seedlings at The Willows Reserve study site were higher in the shaded treatments (0.83) compared to the unshaded (M-S = 0.11; H-S = 0.35; C-S = 0.72) and control (0.02) (Figure 4-18A). The statistical analyses in

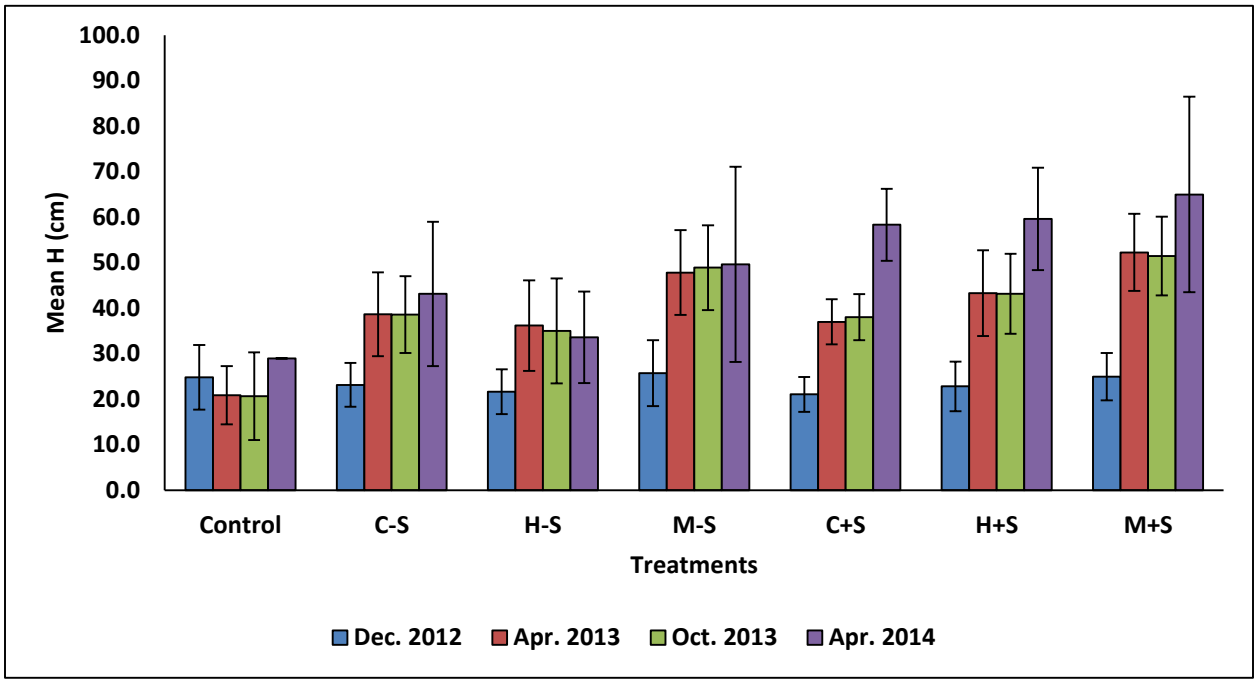


Figure 4-19 Mean heights (cm) of *Pittosporum tenuifolium* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. The Willows Reserve.

Table 4-17 indicate that survival was higher in the shaded treatments than in the control in 100% of the simulations (P = 1.00). Probability of survival was also more elevated in the unshaded plots than in the control (P ≥ 0.93). However, the combination of grass removal and shade was more expressive than grass removal alone (P ≥ 0.77). *P. tenuifolium* seedlings had better establishment results in the C+S compared to H+S ($P_{C+S|H+S}$ = 0.84) and M+S ($P_{C+S|M+S}$ = 0.98). Probability of seedling survival was lower in the absence of shade compared to the shaded treatments (P ≤ 0.23). Among the unshaded treatments, C-S offered better probability of survival than H-S ($P_{C-S|H-S}$ = 0.97) and M-S ($P_{C-S|M-S}$ = 1.00).

Figure 4-19 shows that *P. tenuifolium* seedlings increased in mean heights between planting and April-2013 under all treatments except control. Initial values ranged from 21.1 to 25.7 cm and, in

April-2013, mean heights were between 20.9 (control) to 52.3 cm (M+S). Between April and October-2013, mean heights of seedlings reduced under most treatments, except in the M-S and C+S. Seedlings resumed growth in the following period under most treatments, except in the H-S where seedlings had dieback instead. At the end of the experiment, average seedling heights ranged from 29.0 cm to 65.0 cm.

RHI values of *P. tenuifolium* seedlings were positive under all treatments (Figure 4-18B). Simulations in Table 4-18 show a marked treatment effect on RHI of *P. tenuifolium* seedlings compared to the control ($P \geq 0.81$). The combination of shade and grass removal had stronger effect on this parameter than grass removal alone in over 86% of the tests. Differences among grass removal methods in the shaded treatments were only substantial between C+S and M+S ($P_{C+S|M+S} = 0.77$). C+S also resulted in higher RHI than H+S, though differences between these two treatments may be considered small ($P_{C+S|H+S} = 0.62$). The same inference can be drawn from the comparison between H+S and M+S ($P_{H+S|M+S} = 0.62$). Seedling growth in the unshaded treatments were markedly higher in the M-S plots than in the C-S ($P_{M-S|C-S} = 0.80$). RHI were also higher in the M-S than in the H-S ($P_{M-S|H-S} = 0.74$). H-S and C-S had relatively similar effects on this parameter ($P_{H-S|C-S} = 0.54$). Although growth probabilities in the M-S treatment were higher than in the other unshaded treatments they were still expressively lower than in the shaded treatments ($P \leq 0.14$).

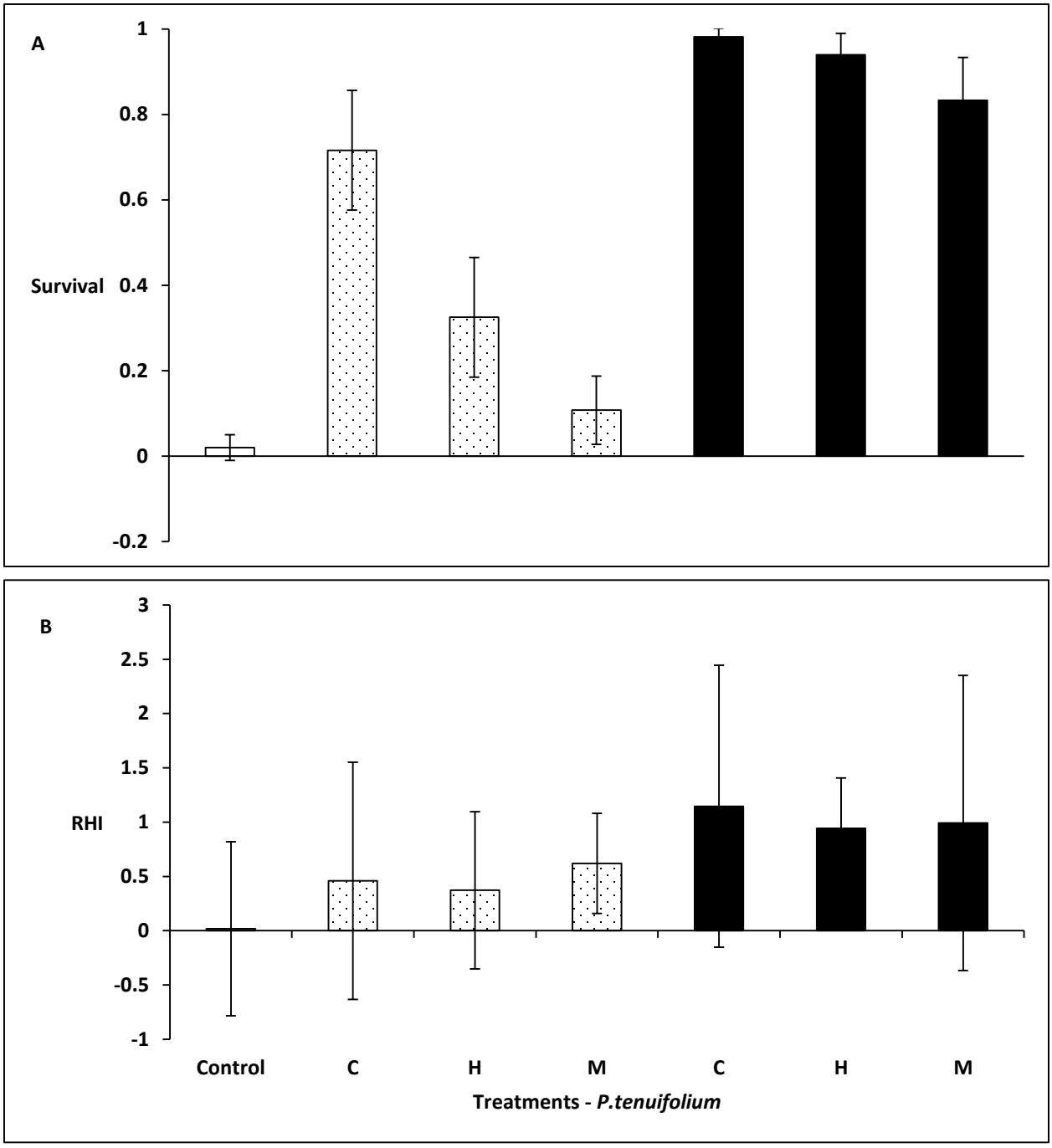


Figure 4-18 Estimated probability of survival (A) and Relative Height Increment (B), and respective 95% credible intervals, for *Pittosporum tenuifolium* seedlings per treatment. Pattern fill – grass removal treatments without shade. Solid fill – grass removal and shade treatments. C – cultivation, H – herbicide, M – mulch. Willows Reserve.

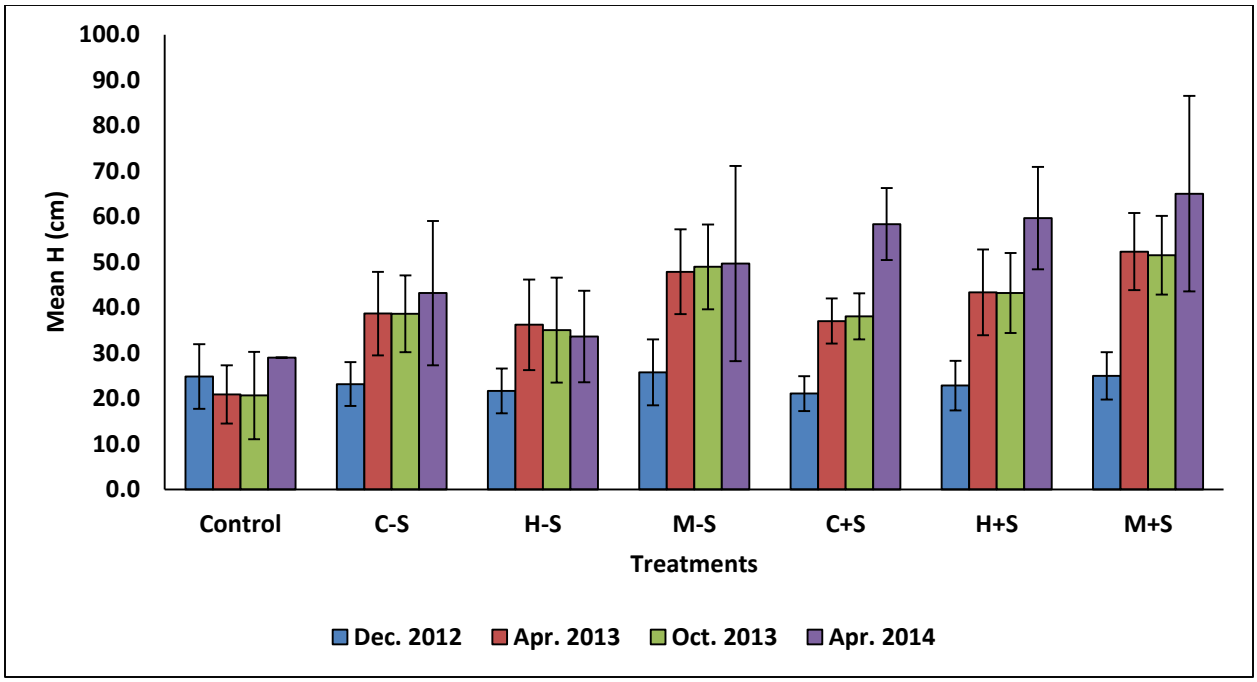


Figure 4-19 Mean heights (cm) of *Pittosporum tenuifolium* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. The Willows Reserve.

Table 4-17 Comparison of estimated probability of survival for *Pittosporum tenuifolium* among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(estS_A > estS_B|data)$, where estS refers to estimated probability of survival. Willows Reserve.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	1.00	0					
H-S	1.00	0.03	0				
M-S	0.93	0.00	0.08	0			
C+S	1.00	1.00	1.00	1.00	0		
H+S	1.00	0.96	1.00	1.00	0.16	0	
M+S	1.00	0.77	0.99	1.00	0.03	0.13	0

Table 4-18 Comparison of estimated RHI of *Pittosporum tenuifolium* seedlings among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(RHI_A > RHI_B|data)$. Willows Reserve.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.81	0					
H-S	0.82	0.54	0				
M-S	0.90	0.80	0.74	0			
C+S	0.99	1.00	1.00	0.95	0		
H+S	0.97	0.99	0.99	0.91	0.38	0	
M+S	0.98	0.99	0.99	0.86	0.23	0.38	0

4.2.4 Chlorophyll Fluorescence

The analysis shows that average chlorophyll fluorescence readings (Y-values) of *K. robusta* and *P. tenuifolium* seedlings fluctuated throughout the experimental period, following a relatively similar pattern and varying along with the seasons. Higher Y-values of both species tended to occur in the summer, then decreasing in early spring, a trend observed in the first and second years. *K. robusta* seedlings had estimated Y-values ≥ 610.1 and *P. tenuifolium* seedlings had Y-values ≥ 545.7, on average, during the experimental period. Average chlorophyll fluorescence readings of both species were higher in the second summer than in the first (Figure 4-20).

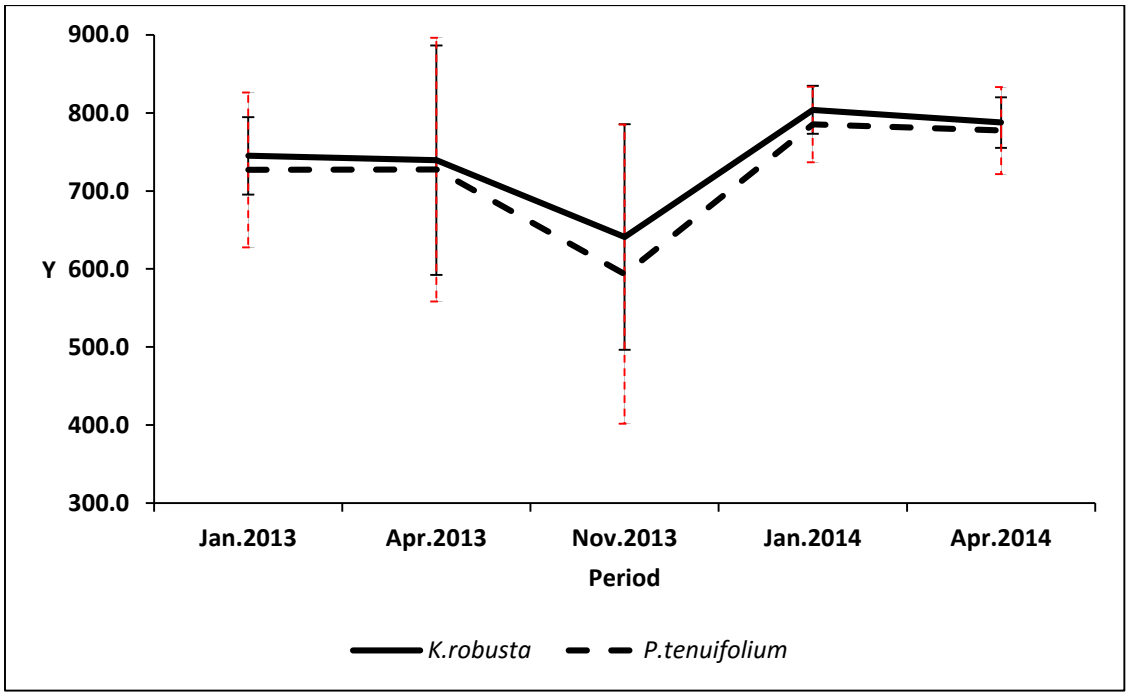


Figure 4-20 Average Y-values and respective 95% credible intervals of *Kunzea robusta* and *Pittosporum tenuifolium* seedlings throughout the experiment period. Willows Reserve.

Kunzea robusta

Average Y-values in January-2014 ranged from 608.9 (control) to 831.2 (M+S) and were generally higher in the shaded than in the control and unshaded treatments (Figure 4-21). The results of the statistical analyses in Table 4-19 show a strong treatment effect on this parameter compared to control (P = 1.00). Estimated Y-values of seedlings planted in the H+S were not statistically larger than in the H-S ($P_{H+S|H-S}$ = 0.49). Comparisons among grass removal methods combined with shade showed H+S and C+S had similar effects on estimated Y-values ($P_{H+S|C+S}$ = 0.50), whereas averages in the M+S were higher than in the C+S and H+S ($P_{M+S|C+S}$ = 0.65, $P_{M+S|H+S}$ = 0.64), although only marginally. Estimated Y-values of *K. robusta* seedlings were markedly higher in the H-S compared to M-S and C-S (P ≥ 0.98).

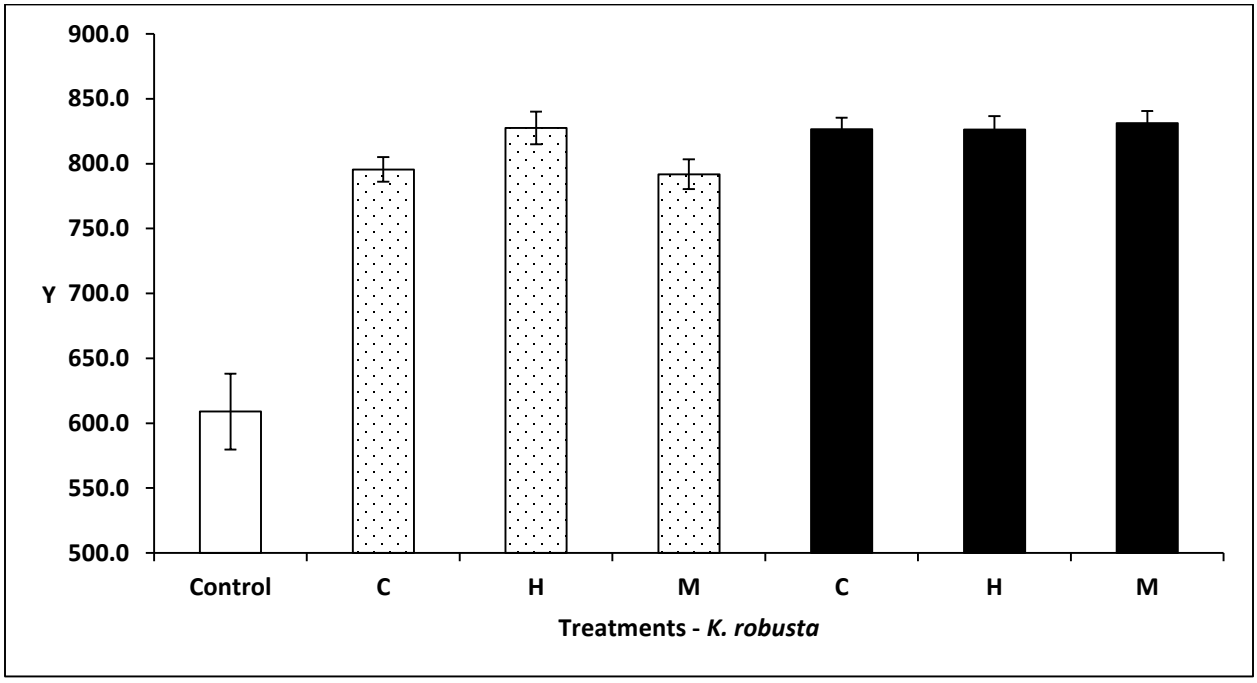


Figure 4-21 Estimated Y-values and respective 95% credible intervals for *Kunzea robusta* seedlings, per treatment, in January-2014: Pattern fill – grass removal and no-shade treatments. Solid fill – grass removal and shade treatments. Willows Reserve.

Pittosporum tenuifolium

Estimated Y-values of *P. tenuifolium* seedlings in January-2014 ranged from 668.4 (control) to 802.9 (C+S), and seedlings had higher averages in the shaded treatments compared to the control plots, as well as to most unshaded treatments, excepting in the M+S, where seedlings had lower average Y-values than H-S and M-S (Figure 4-22). The statistical analyses showed a substantial treatment effect on estimated chlorophyll fluorescence readings in this period ($P \geq 0.99$; Table 4-20). Estimated Y-values in the C+S were markedly higher than in the C-S ($P_{C+S|C-S} = 0.95$), as were in the H+S compared to H-S ($P_{H+S|H-S} = 0.78$). Averages in the M+S were statistically similar to those of the C-S plots ($P_{M+S|C-S} = 0.51$), and markedly lower than those of the C+S ($P_{M+S|C+S} = 0.04$) and H+S ($P_{M+S|H+S} = 0.08$). Average Y-values in the M+S were also lower than those obtained by seedlings in the H-S ($P_{M+S|H-S} = 0.24$) and M-S treatments ($P_{M+S|M-S} = 0.39$). Although estimated Y-values of C+S were higher than in the H+S, differences may be considered small ($P_{C+S|H+S} = 0.67$). Grass removal in the absence of shade had a stronger effect on estimated Y-values of seedlings in the H-S compared to those in the C-S ($P_{H-S|C-S} = 0.74$). Differences in estimated Y-values in the M-S compared to H-S ($P_{M-S|H-S} = 0.43$) and to C-S ($P_{M-S|C-S} = 0.62$) may be considered statistically irrelevant.

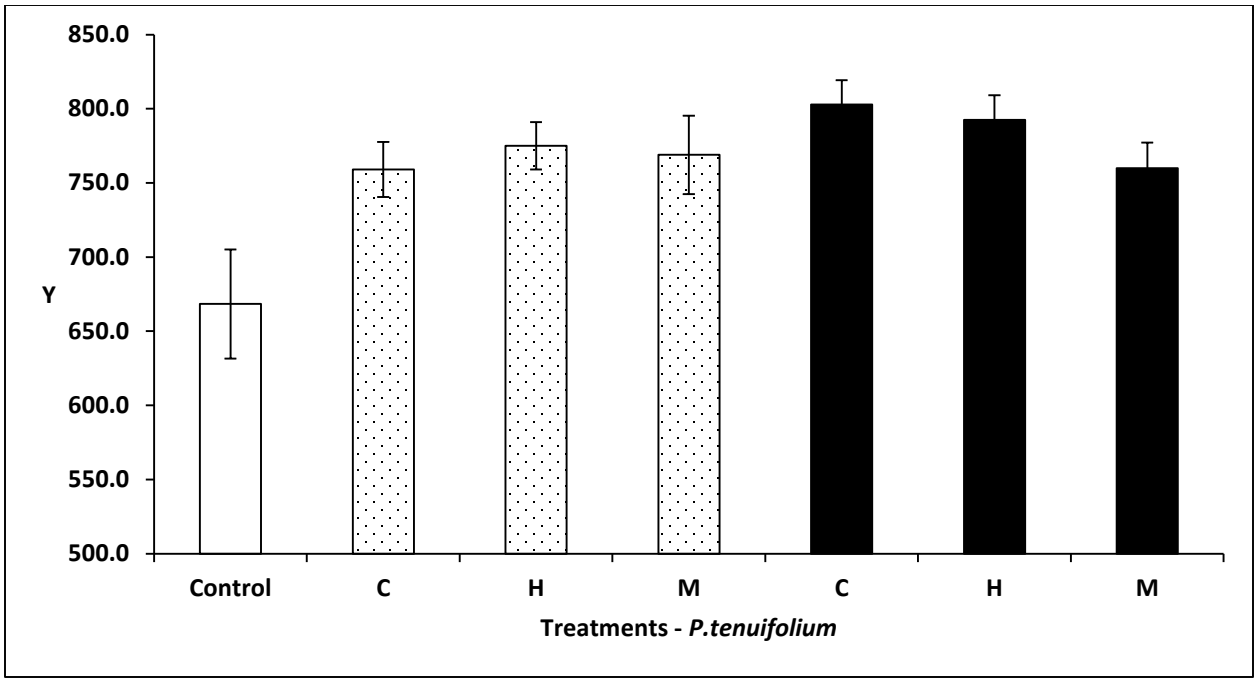


Figure 4-22 Estimated Y-values and respective 95% credible intervals for *Pittosporum tenuifolium* seedlings, per treatment, in January-2014: Pattern fill – grass removal and no-shade treatments. Solid fill – grass removal and shade treatments. Willows Reserve.

Table 4-19 Comparison of estimated Y-values of *Kunzea robusta* seedlings among treatments in January-2014. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(Y_A > Y_B|data)$, where Y refers to estimated chlorophyll fluorescence. Willows Reserve.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	1.00	0					
H-S	1.00	0.98	0				
M-S	1.00	0.41	0.02	0			
C+S	1.00	0.99	0.47	0.99	0		
H+S	1.00	0.99	0.46	0.99	0.50	0	
M+S	1.00	1.00	0.59	1.00	0.65	0.64	0

Table 4-20 Comparison of estimated Y-values of *Pittosporum tenuifolium* seedlings among treatments in January-2014. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(Y_A > Y_B|data)$, where Y refers to estimated chlorophyll fluorescence. Willows Reserve.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.99	0					
H-S	1.00	0.74	0				
M-S	0.99	0.62	0.43	0			
C+S	1.00	0.95	0.89	0.86	0		
H+S	1.00	0.90	0.78	0.77	0.33	0	
M+S	0.99	0.51	0.24	0.39	0.04	0.08	0

4.2.5 Carbon Isotope Analysis - $\delta^{13}C$

Since only one *K. robusta* seedling was found in the control plots at the end of the experiment, and this individual had few leaves left, it was decided not to collect any leaf samples from that plant to avoid any more stress on that individual. Therefore, statistical analyses and further discussion of the results were limited to the six treatments: C-S, H-S, M-S, C+S, H+S, and M+S. Estimated $\delta^{13}C$ values of *Kunzea robusta* seedlings ranged from -28.07‰ to -31.15‰ (Figure 4-23) and were more negative in the shaded treatments, though no strong statistical differences among most treatments could be detected (P = 0.32 ~ 0.64). Except for C-S, which showed slightly higher (less negative) estimated $\delta^{13}C$ values than in the H+S or in the M+S treatments in 72% of the simulations (Table 4-21). The statistical analysis of estimated $\delta^{13}C$ of *P. tenuifolium* seedlings were performed only for the seedlings found in the C-S, H-S, M-S, C+S, H+S, and M+S treatments. Estimated $\delta^{13}C$ values varied from -27.32‰ to -30.23‰ (Figure 4-24) and tended to be more negative in the shaded treatments (Table 4-22). Estimated $\delta^{13}C$ in the H+S were relatively larger than in the H-S (P = 0.71). Differences among the remaining treatments may be considered insubstantial (P = 0.47 ~ 0.69).

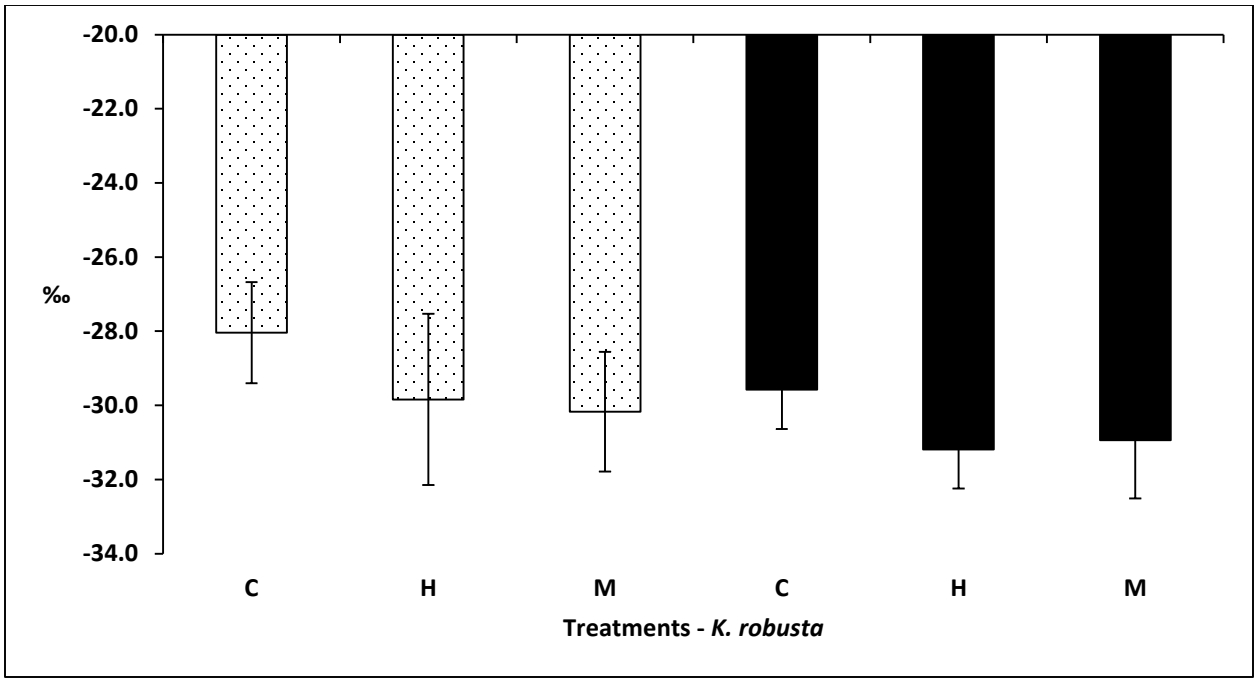


Figure 4-23 Estimated $\delta^{13}C$ values and respective 95% credible intervals for *Kunzea robusta* seedlings per treatment: Pattern fill – grass removal and no-shade treatments. Solid fill – grass removal and shade treatments. Willows Reserve.

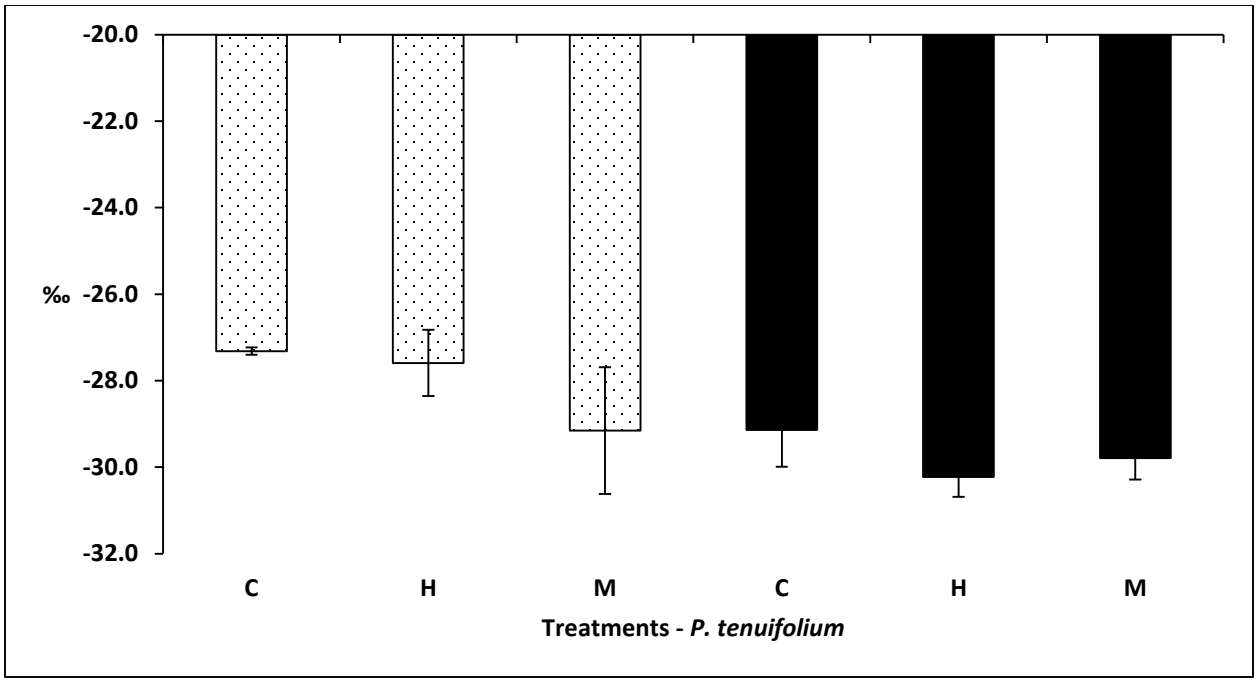


Figure 4-24 Estimated $\delta^{13}C$ values and respective 95% credible intervals for *Pittosporum tenuifolium* seedlings per treatment: Pattern fill – grass removal and no-shade treatments. Solid fill – grass removal and shade treatments. Willows Reserve.

Table 4-21 Comparison of estimated $\delta^{13}C$ values of *Kunzea robusta* seedlings among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\delta_A > \delta_B|data)$, where δ refers to estimated $\delta^{13}C$ values. Willows Reserve.

Treatment	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
C-S	0					
H-S	0.61	0				
M-S	0.68	0.50	0			
C+S	0.61	0.46	0.44	0		
H+S	0.72	0.55	0.58	0.61	0	
M+S	0.72	0.57	0.58	0.64	0.52	0

Table 4-22 Comparison of $\delta^{13}C$ values of *Pittosporum tenuifolium* seedlings among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\delta_A > \delta_B|data)$, where δ refers to estimated $\delta^{13}C$ values. Willows Reserve.

Treatment	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
C-S	0					
H-S	0.55	0				
M-S	0.62	0.60	0			
C+S	0.62	0.59	0.49	0		
H+S	0.69	0.71	0.59	0.60	0	
M+S	0.69	0.67	0.57	0.57	0.47	0

4.3 Dierickx Farm

4.3.1 Weather Data

The weather data for the Dierickx Farm trial were obtained from Lake Tekapo EWS and Lake Tekapo Air Safaris weather stations (Cliflo: http://cliflo.niwa.co.nz). The total amount of precipitation (P_{total}) for the 17 month-trial in the Tekapo region was 843.2 mm, or monthly averages equal to 49.6 mm, mostly concentrated in May and June-2013 (232.5 mm or 27.6% of P_{total}). April-2013 received the lowest amount of rain for the period (10.7 mm). The 2013 calendar year received 667.2 mm or 79.1% of P_{total} (Figure 4-25), which was higher than the long-term average of 580.1 mm between 1994 and 2014 registered by Lake Tekapo EWS and Lake Tekapo Air Safaris weather stations (https://www.niwa.co.nz). Monthly average maximum air temperature was 16.6°C, and the average minimum temperature was 4.2°C. February-2013 experienced the highest air temperature (23.9 °C), whereas the lowest temperature was registered in June-2013 (-3.2°C; Table 4-23).

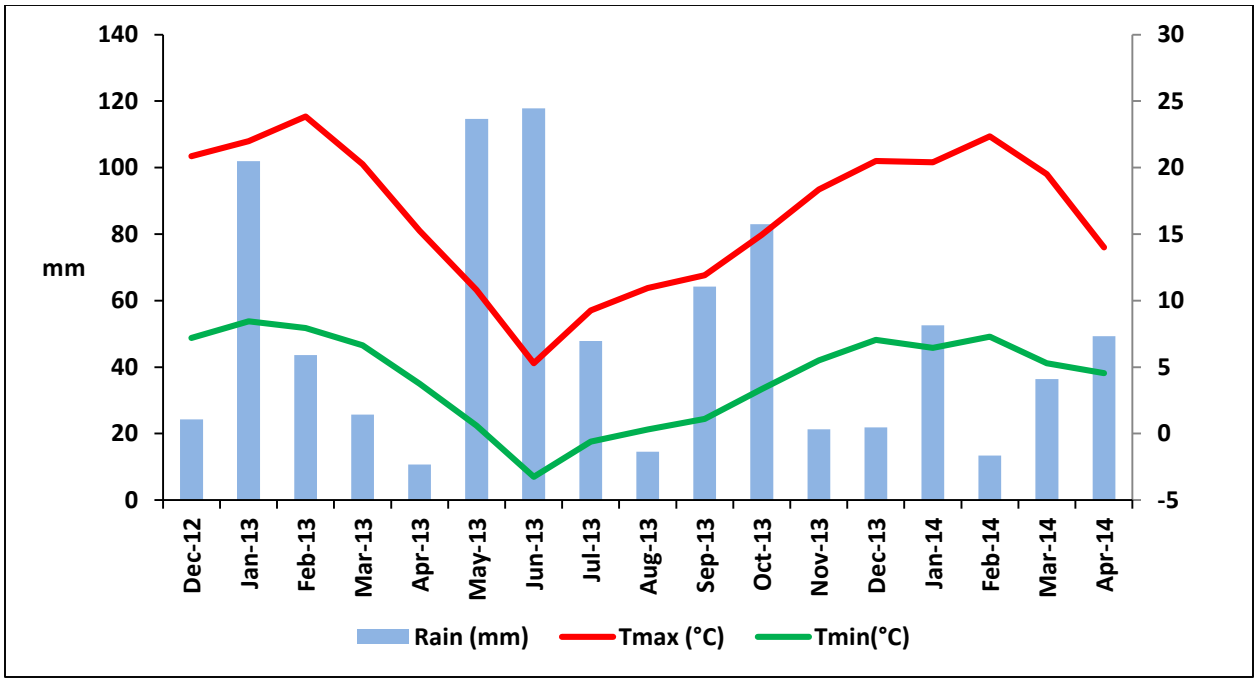


Figure 4-25 Monthly weather averages for Tekapo Region for the experimental period. Tmax – maximum air temperature, Tmin – minimum air temperature. Source: http://cliflo.niwa.co.nz.

Table 4-23 Weather data summary for the experimental period with averages, standard deviations (sd), maximum and minimum readings for Tekapo region. Tmax – maximum air temperature, Tmin – minimum air temperature. Source: http://cliflo.niwa.co.nz.

Statistical Parameters	**Rain (mm)**	**Tmax (°C)**	**Tmin (°C)**
Average	49.6	16.5	4.2
sd	34.3	5.2	3.3
Max	117.9	23.9	8.5
Min	10.7	5.3	-3.25

4.3.2 Soil water Content

Average soil water content (Θ) at Dierickx Farm fluctuated throughout the experimental period, with lower estimated Θ levels in the summer months (December-2012 and January-2014) and highest levels in October-2013, or mid-spring. Averages were normally < 30%, except for H+S in April-2013 (31.3%) and for all treatments in October-2013 (Θ ~ 39.4% to 47.5%). Averages under the treatments in the summer monitoring periods were mostly < 20%. (Figure 4-26). Soil moisture content at planting in December-2012 was ≤ 13% and relatively homogenous across the study site and under all treatments (P = 0.47 ~ 0.58). The total precipitation that month was 24.3 mm and approximately 0.3 mm of rain was registered in the 15 days prior to soil samples being collected. Average monthly air temperatures ranged between 7.2°C and 20.8°C, and average monthly relative air humidity was 59.2%, the lowest of the trial. On the day of soil sampling (23/12/2012), the maximum air temperature was 22.8°C.

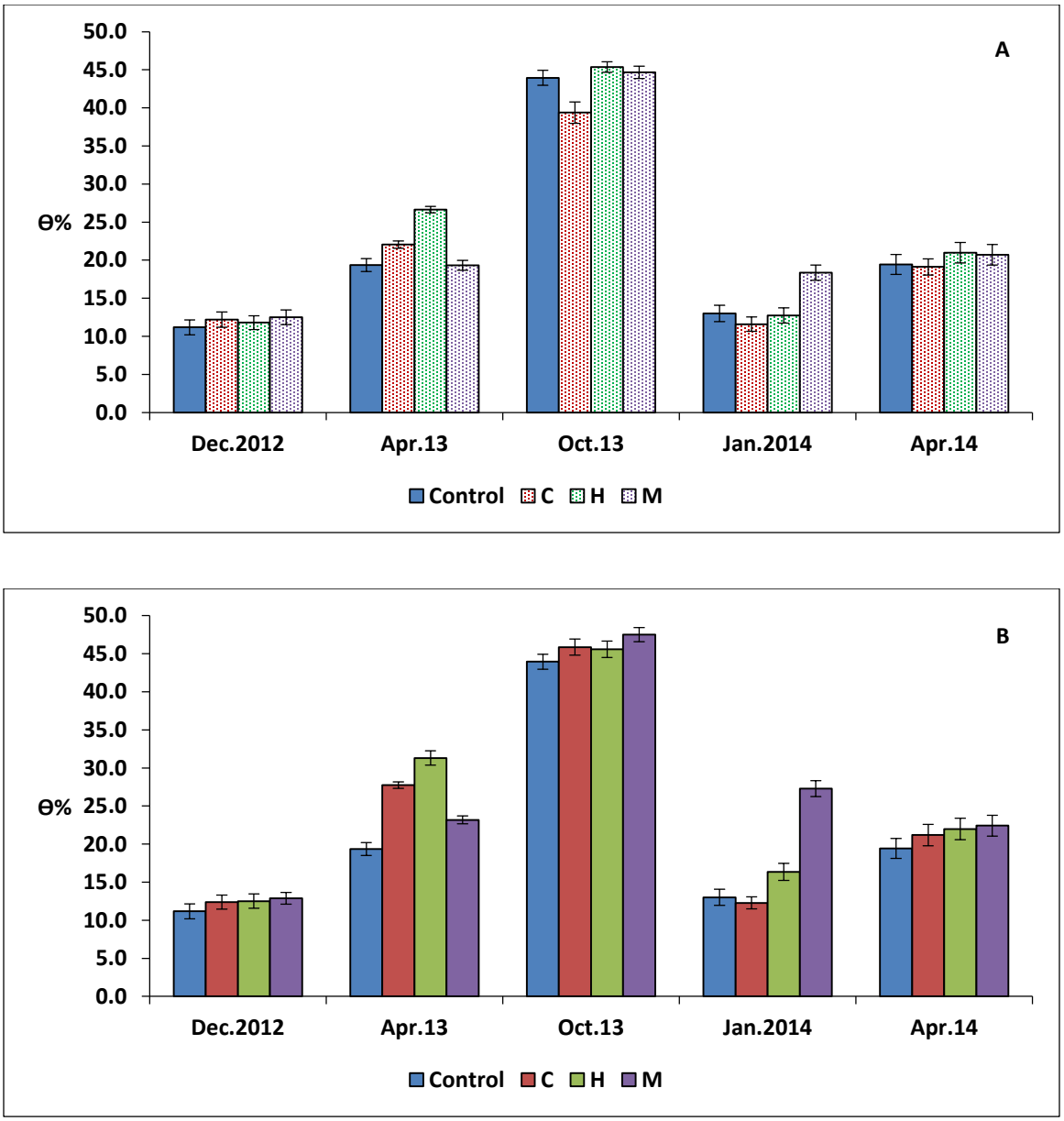


Figure 4-26 Average soil water content and respective 95% credible intervals per treatment in each monitored period. A - control and grass removal treatments without shade; B - control and grass removal treatments with shade. C – cultivation, H – herbicide, M – mulch. Dierickx Farm.

The total amount of rain in January-2014 was 56.6 mm, and a total of 2.7 mm of rain was recorded in the 15 days that preceded soil sampling. However, there was no rain on the day (18/01/2014) or on the last five days prior to soil moisture monitoring. Average monthly air temperatures ranged from 6.4°C to 20.4°C, and average monthly relative air humidity was 59.3%. The highest air temperature registered on the day of soil sampling was 24.3°C. Average soil water content under most treatments in January-2014 was < 20%, except in the M+S treatment (Figure 4-27). Θ in the M+S and M-S treatments were markedly higher than under the other treatments (Table 4-24). Θ level in the M+S treatment was significantly higher than in the control ($P_{M+S|control} = 0.90$), as well as statistically more elevated than in the C+S and H+S ($P \geq 0.83$), and also higher than in the three grass-removal-only treatments ($P \geq 0.79$). Estimated Θ in the H+S were also markedly higher than in the C+S ($P_{H+S|C+S} = 0.70$). Among the grass-removal-only treatments, Θ was markedly higher in the M-S compared to C-S ($P_{M-S|C-S} = 0.75$) and to H-S ($P_{M-S|H-S} = 0.71$), whereas differences between C-S and H-S were statistically irrelevant ($P_{C-S|H-S} = 0.52$). Θ levels in the M-S were higher than in the C+S ($P_{M-S|C+S} = 0.78$), but relatively similar to H+S treatment ($P_{M-S|H+S} = 0.58$). Comparing C+S to C-S ($P_{C+S|C-S} = 0.46$), and H+S to H-S ($P_{H+S|H-S} = 0.64$), it is accurate to say that differences in the estimated Θ were not substantial. Overall, Θ levels were generally higher in the shaded treatments, although differences between shaded and unshaded treatments were statistically irrelevant ($P = 0.44 \sim 0.66$), with the exception of M+S which presented the highest estimated Θ level of the period.

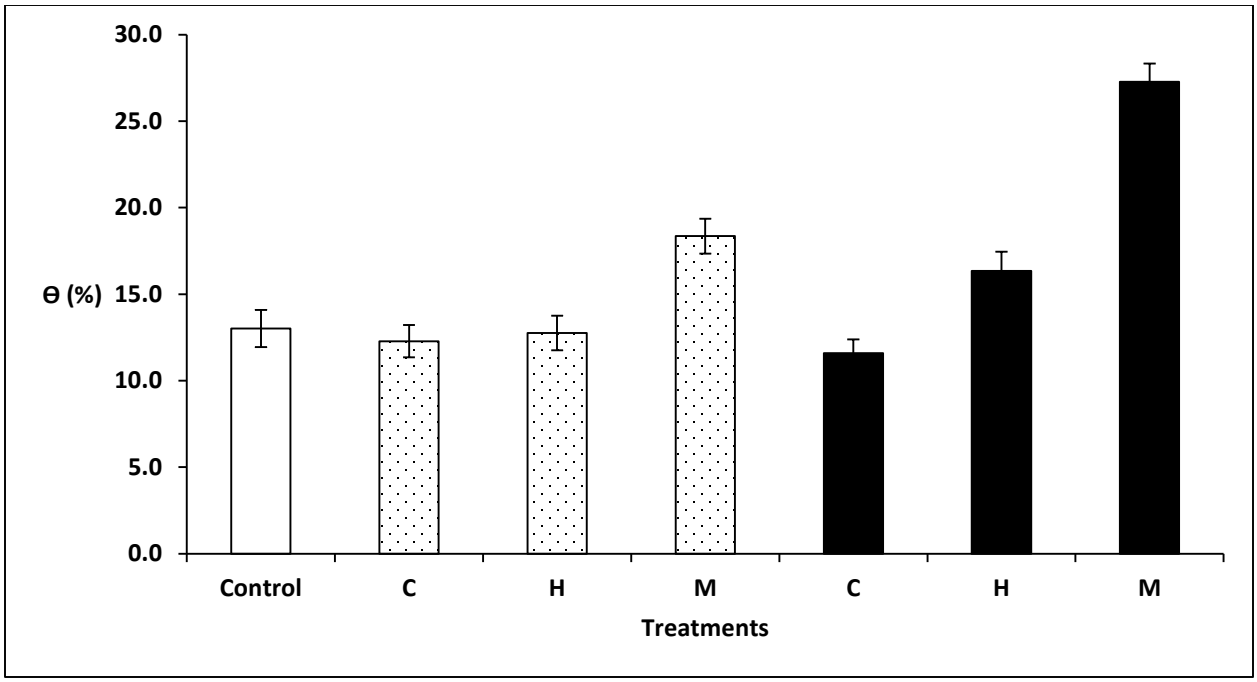


Figure 4-27 Estimated soil water content and respective 95% credible intervals, per treatment, in January-2014. Pattern fill – grass removal treatments without shade. Solid fill – grass removal treatments with shade. Dierickx Farm.

Table 4-24 Comparison of estimated soil water content among treatments in January-2014. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\Theta_A > \Theta_B|data)$, where Θ refers to estimated soil water content. Dierickx Farm.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.47	0					
H-S	0.50	0.52	0				
M-S	0.71	0.75	0.71	0			
C+S	0.46	0.46	0.45	0.22	0		
H+S	0.64	0.66	0.64	0.42	0.70	0	
M+S	0.90	0.91	0.90	0.79	0.94	0.83	0

4.3.3 Survival and Growth

A total of 68 (32.4%) *Leptospermum scoparium* and 109 (51.9%) *Ozothamnus leptophyllus* seedlings survived until the end of the experiment at Dierickx Farm. The largest proportion of survivors of both species was in the shaded treatments. M+S had the highest number of *L. scoparium* seedlings (20 individuals), whilst the majority of *O. leptophyllus* seedlings were found in the C+S and H+S treatments, both with 22 individuals in each. M-S had the lowest number of surviving *O. leptophyllus* seedlings (7). No *L. scoparium* seedlings were found in the control plots at the end of the trial, and only three remained in the M-S treatment (Table 4-25).

Table 4-25 Number of survivors of *Leptospermum scoparium* and *Ozothamnus leptophyllus* seedlings, per treatment. Dierickx Farm.

Treatment	***Leptospermum scoparium***	***Ozothamnus leptophyllus***
Control	0	11
	No shade	
Cultivation	8	16
Herbicide	7	16
Mulch	3	7
	Shade	
Cultivation	15	22
Herbicide	14	22
Mulch	20	15
Total	69	109

Leptospermum scoparium

Estimated probability of survival of *L. scoparium* seedlings were below 67%. Seedlings had higher probabilities in the shaded treatments (Figure 4-28A), with highest survival in the M+S treatment (0.67) followed by C+S (0.49) and H+S (0.43). *L. scoparium* seedlings in the grass-removal-only treatments had estimated probability of survival ranging from 0.21 (H-S) to 0.07 (M-S), and zero probability in the control plots. The analyses in Table 4-26, therefore, show that the shaded treatments offered the highest probability of survival for *L. scoparium* seedlings compared to control (P = 1.00). Comparisons also indicate that seedlings had higher probability of surviving in the shaded treatments instead of in the unshaded plots ($P \geq 0.85$). M+S was more effective than C+S ($P_{M+S|C+S} = 0.77$) and H+S ($P_{M+S|H+S} = 0.82$). Differences between probabilities in the H+S and C+S were statistically irrelevant ($P_{H+S|C+S} = 0.57$). In the absence of shade, probability of survival of *L. scoparium* seedlings were still expressively higher than in the control (P = 0.81 ~ 0.97). Probabilities in the H-S the C-S were greater than in the M-S ($P_{H-S|M-S} = 0.87$ and $P_{C-S|M-S} = 0.80$), whereas the effects of H-S and C-S on the seedlings' probability of survival may be considered statistically similar ($P_{H-S|C-S} = 0.53$).

Figure 4-29 shows that at planting *L. scoparium* seedlings had mean heights ranging from 34.0 cm to 38.7 cm, and their average heights increased between planting and April-2013 about 8.0 cm (M-S) to 16.6 cm (C+S), whilst seedlings in the control plots had a decrease in average heights of 0.05 cm, on average, during the same period. No height increment was registered between April and October-2013, when *Leptospermum scoparium* seedlings had dieback under all treatments, and mean heights in October-2013 ranged from 16.0 cm (M-S) to 46.8 cm (C+S), and no *L. scoparium* seedlings were found in the control plots. Increases in seedling mean heights were recorded in the following season, from October-2013 to April-2014, under most treatments, except in the C-S where seedlings lost, on average, 9.5 cm in height. At the end of the experiment, seedlings had mean heights ranging from 23.0 cm (C-S and M-S) to 53.2 cm (M+S).

RHI values under most treatments were positive, except in the M-S and C-S (Figure 4-28B). Seedling growth was greater in the shaded treatments, with highest values calculated for the M+S. The statistical analyses did not include the control plots (Table 4-27) and show that the

combination of shade and grass removal had a markedly stronger effect on seedling growth than grass removal only ($P \geq 0.73$). RHI were higher in the M+S compared to the grass-removal-only treatments ($P \geq 0.88$). Seedlings also had higher estimated RHI in the M+S compared to the C+S ($P_{M+S|C+S} = 0.75$), but relatively similar to H+S ($P_{M+S|H+S} = 0.57$). C+S was more effective than the unshaded treatments ($P \geq 0.73$). RHI in the H+S were also expressively larger than in the grass-removal-only treatments ($P \geq 0.84$). There were no large differences in treatment effect on estimated RHI among the grass-removal-only treatments ($P = 0.43 \sim 0.67$).

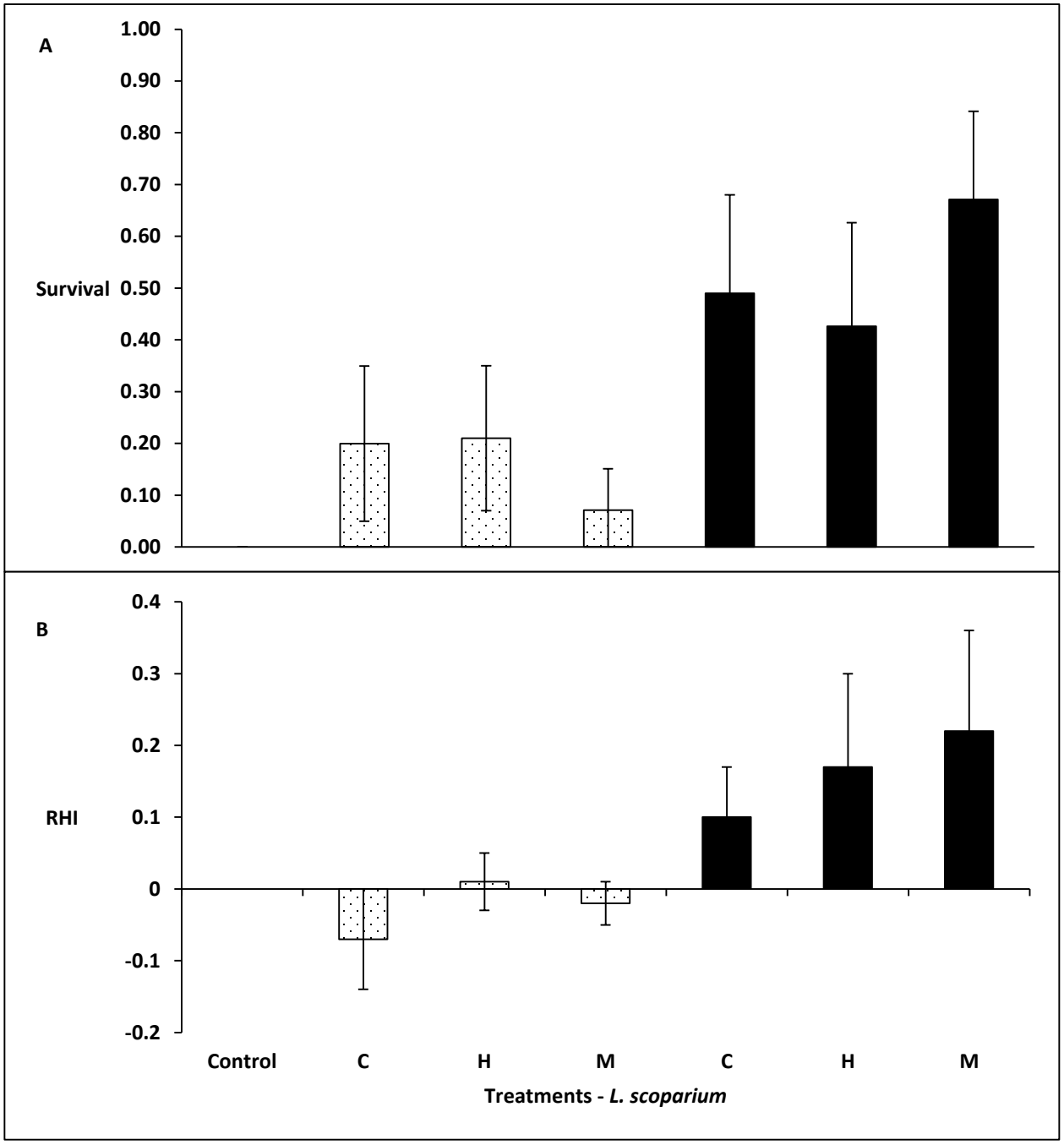


Figure 4-28 Estimated probabilities of survival (A) and Relative Height Increment (B), and respective 95% credible intervals, per treatment, for *Leptospermum scoparium* seedlings. C – cultivation, H – herbicide, M – mulch. Pattern fill: grass removal without shade. Solid fill: grass removal with shade. Dierickx Farm.

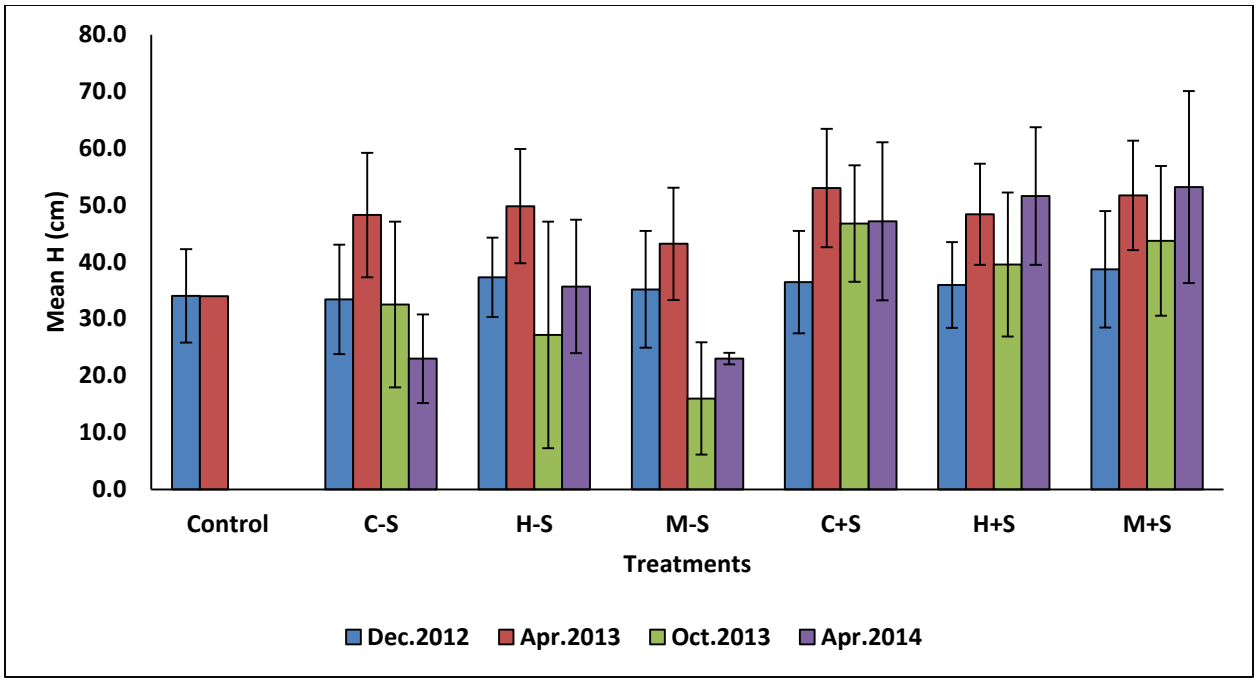


Figure 4-29 Mean heights (cm) of *Leptospermum scoparium* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. Dierickx Farm.

Table 4-26 Comparison of estimated probability of survival of *Leptospermum scoparium* seedlings among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(estS_A > estS_B|data)$, where estS refers to estimated probability of survival. Dierickx Farm.

Treatment	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
C-S	0					
H-S	0.53	0				
M-S	0.20	0.13	0			
C+S	0.89	0.89	0.98	0		
H+S	0.88	0.85	0.98	0.43	0	
M+S	0.96	0.96	1.00	0.77	0.82	0

Table 4-27 Comparison of estimated RHI among treatments of *Leptospermum scoparium*. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(RHI_A > RHI_B|data)$. Dierickx Farm.

Treatment	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
C-S	0					
H-S	0.67	0				
M-S	0.61	0.43	0			
C+S	0.84	0.73	0.79	0		
H+S	0.93	0.84	0.90	0.67	0	
M+S	0.95	0.88	0.93	0.75	0.57	0

Ozothamnus leptophyllus

Ozothamnus leptophyllus seedlings had estimated probabilities of survival between 0.23 (M-S) and 0.75 (C+S), with highest survival values in the shaded treatments (Figure 4-30A).

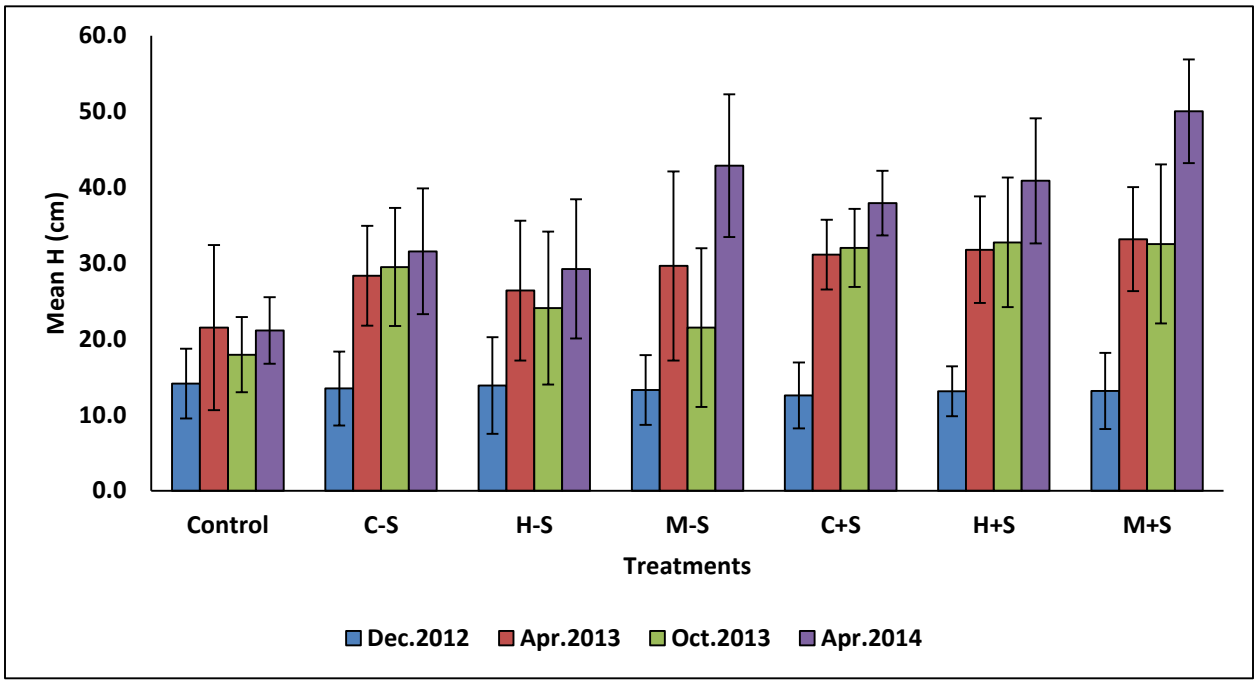


Figure 4-31 Mean heights (cm) of *Ozothamnus leptophyllus* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. Dierickx Farm.

Table 4-28 shows a strong treatment effect on this parameter, with markedly higher survival values in all treatments (except M-S) than in the control ($P \geq 0.79$). Probabilities were higher in the C+S compared to C-S ($P_{C+S|C-S} = 0.89$), and also more elevated in the H+S compared to H-S ($P_{H+S|H-S} = 1.00$). Probabilities of survival under the C+S and H+S were relatively similar ($P_{C+S|H+S} = 0.53$). Although the probability of survival *O. leptophyllus* seedlings in the M+S was markedly higher than in the M-S treatment ($P_{M+S|M-S} = 0.96$), estimated probability of survival in the M+S was still substantially lower than in the other unshaded treatments ($P_{M+S|C-S} = 0.34$; $P_{M+S|H-S} = 0.31$). Probability of survival in the control plots were markedly lower than in the C-S ($P_{control|C-S} = 0.10$) and in the H-S ($P_{control|H-S} = 0.09$), however, they were higher than in the M-S ($P_{control|C-S} = 0.84$), indicating that M-S was the least effective treatment in this trial. Effects of H-S and C-S on seedling survival may be considered statistically similar ($P_{H-S|C-S} = 0.51$).

Figure 4-31 shows *O. leptophyllus* seedlings at the beginning of the experiment had average heights ranging from 12.6 cm to 14.1 cm. In the following measurement period, in April-2013, mean heights had increased under all treatments and ranged from 21.5 cm (control) to 33.2 cm (M+S). In October-2013, mean heights of seedlings in the control (17.93 cm), H-S (24.07 cm), M-S (21.52 cm), and M+S (32.55 cm) treatments had dieback, while those in the C-S (29.51 cm), C+S (32.02 cm), and H+S (32.76 cm) increased in height. Growth was positive for seedlings in all treatments and *O. leptophyllus* seedlings, at the end of the experiment, had average heights varying from 21.1 cm to 50.1 cm.

Relative height increment (RHI) was positive under all treatments. Seedlings had higher estimated RHI in the shaded treatments, whilst the control and M-S plots promoted the lowest growth increment of the trial (Figure 4-30B). The probability of seedling growth was higher in the shaded treatments compared to control ($P \geq 0.91$) and to the grass-removal-only treatments ($P \geq 0.68$; Table 4-29). Seedlings in the C+S had higher estimated RHI than those in the unshaded ($P \geq 0.79$) and control treatments ($P_{C+S|control} = 0.98$). Seedling growth in the C+S was also more pronounced than in the M+S ($P_{C+S|M+S} = 0.70$), but relatively similar to the H+S ($P_{C+S|H+S} = 0.51$). H+S had substantially higher effects on seedling RHI in relation to control ($P_{H+S|control} = 0.95$) and to the grass-removal-only treatments ($P \geq 0.81$). *O. leptophyllus* seedlings also had greater RHI values in the M+S compared to control ($P_{M+S|control} = 0.91$), H-S ($P_{M+S|H-S} = 0.82$) and M-S ($P_{M+S|M-S} = 0.89$). Estimated RHI of seedlings in the M+S was also higher than those in the C-S, however the differences may be considered statistically small ($P_{M+S|C-S} = 0.68$). M-S promoted higher estimated RHI than the control ($P_{M-S|control} = 0.62$), but the differences between these two treatments may be considered weak. Probabilities of seedling growth in the M-S were the lowest of the grass-removal-only treatments ($P \leq 0.41$). Although estimated RHI was higher in the C-S than in the H-S, differences were statistically irrelevant ($P_{H-S|C-S} = 0.34$). Some *O. leptophyllus* seedlings were found with signs of predation on their aboveground structures (Figure 4-32), despite the fact that the study area was fenced off. Figure 4-33 shows two photographs of rabbit or hare excrements found on two different plots at Dierickx Farm.

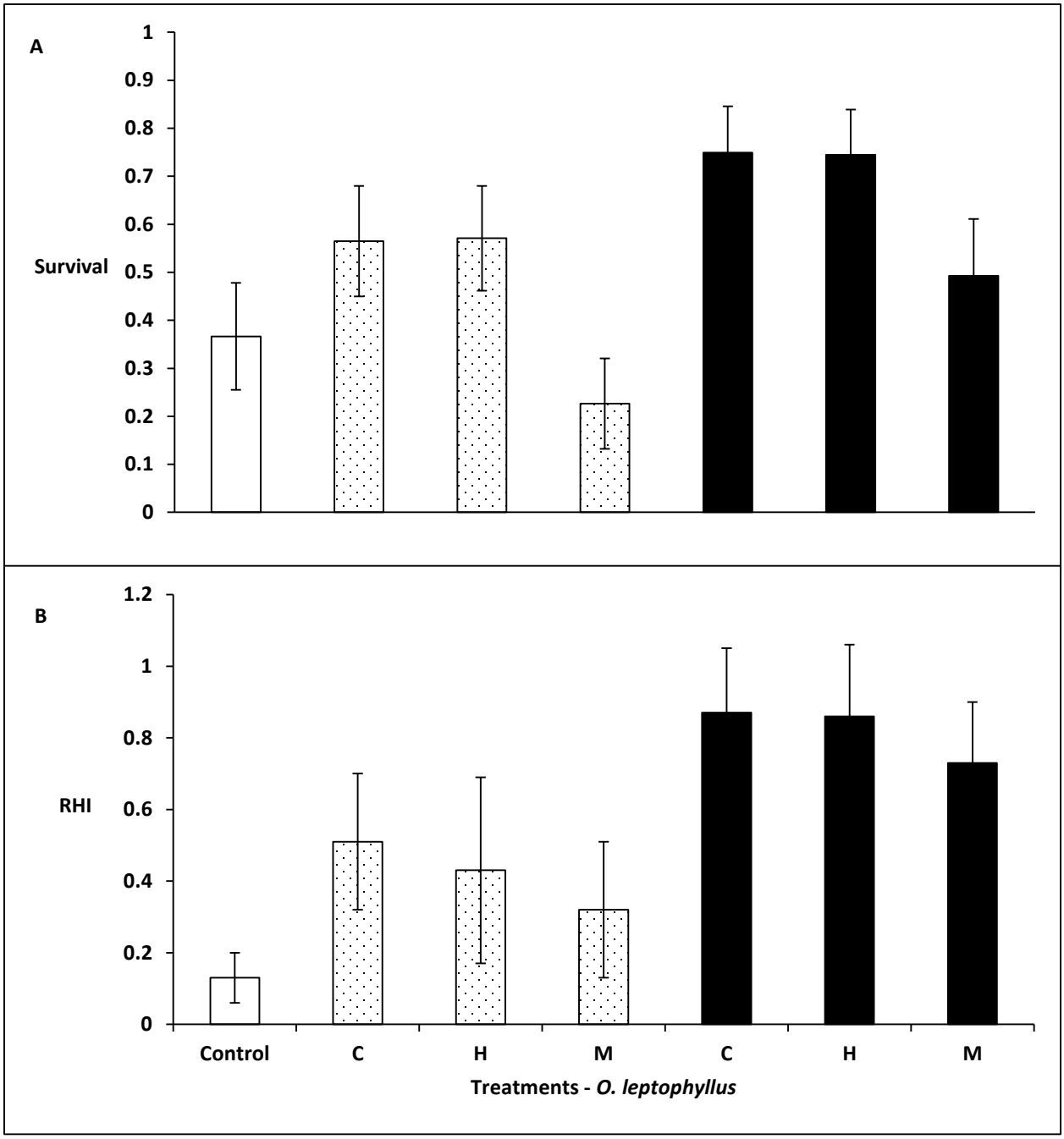


Figure 4-30 Estimated probabilities of survival (A) and Relative Height Increment (B), and respective 95% credible intervals, per treatment, for *Ozothamnus leptophyllus* seedlings. C – cultivation, H – herbicide, M – mulch. Pattern fill: grass removal without shade. Solid fill: grass removal with shade. Dierickx Farm.

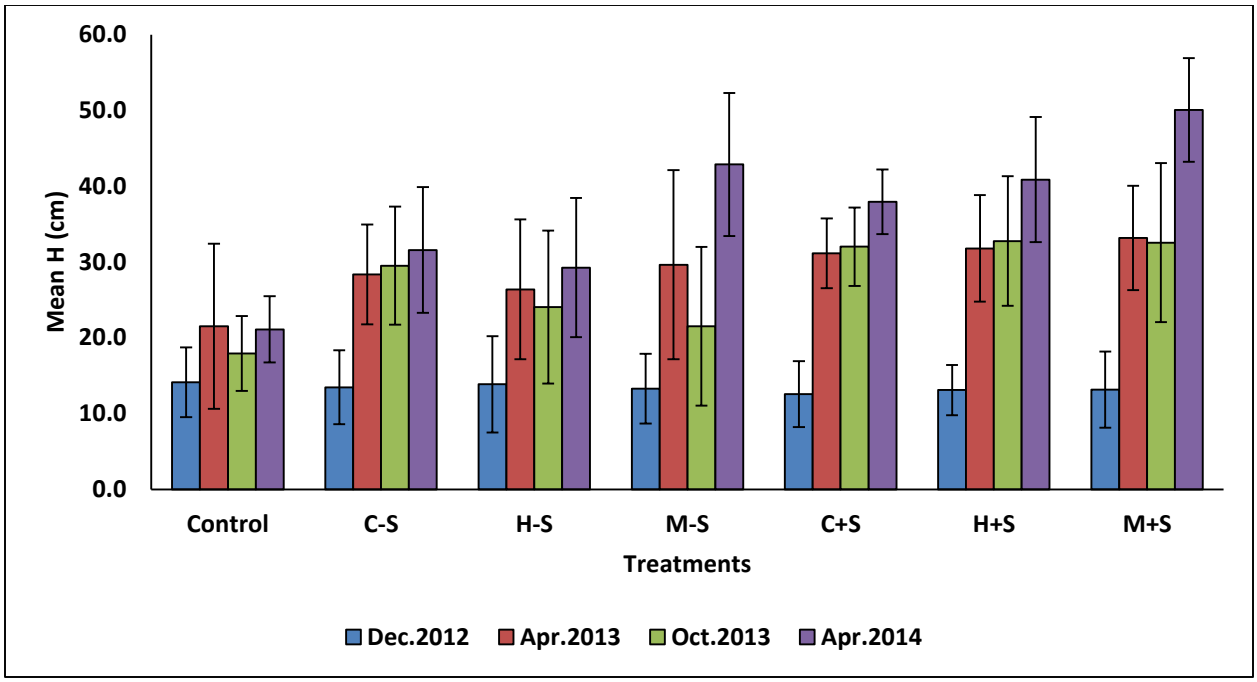


Figure 4-31 Mean heights (cm) of *Ozothamnus leptophyllus* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. Dierickx Farm.

Table 4-28 Comparison of estimated probability of survival (P) of *Ozothamnus leptophyllus* seedlings among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(estS_A > estS_B|data)$, where estS refers to estimated probability of survival. Dierickx Farm.

Treatment	Control	C-S	H-S	M-S	C+S	H+S	M+S
Control	0						
C-S	0.90	0					
H-S	0.91	0.51	0				
M-S	0.16	0.01	0.01	0			
C+S	0.99	0.89	0.89	1.00	0		
H+S	1.00	0.89	0.89	1.00	0.47	0	
M+S	0.79	0.34	0.31	0.96	0.04	0.04	0

Table 4-29 Comparison of estimated RHI of *Ozothamnus leptophyllus* seedlings among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(RHI_A > RHI_B|data)$. Dierickx Farm.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.85	0					
H-S	0.71	0.34	0				
M-S	0.62	0.25	0.41	0			
C+S	0.98	0.79	0.89	0.96	0		
H+S	0.95	0.81	0.88	0.92	0.49	0	
M+S	0.91	0.68	0.82	0.89	0.30	0.31	0

Figure 4-32 One *Ozothamnus leptophyllus* seedling in a mulch-and-shade (M-S) plot. Branches seem to have been browsed on. Dierickx Farm.

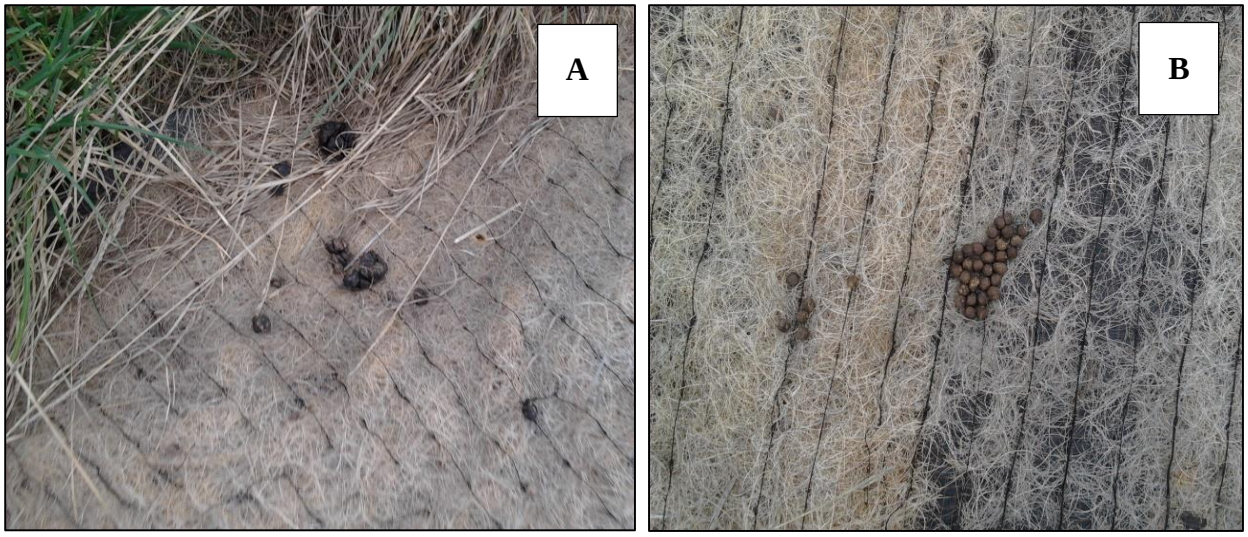


Figure 4-33 Feces found in a mulch-and-shade plot (A) and on a mulch-no-shade plot (B) that provide evidence of the presence of rabbits or hare in the study site. Dierickx Farm.

4.3.4 Chlorophyll Fluorescence

Estimated chlorophyll fluorescence readings (Y-values) of *L. scoparium* and *O. leptophyllus* seedlings fluctuated throughout the experimental period, in a similar pattern, with highest averages in the summer, decreasing in autumn, reaching the lowest values in mid-spring, and then rising again in mid-summer (Figure 4-34). Estimated Y-values of *L. scoparium* seedlings were ≥ 600 during most of the trial, but averages plummeted in November-2013 (Y-value = 634.4) when fluorescence readings of many seedlings were ≤ 500. Average Y-values of *O. leptophyllus* seedlings were ≥ 780 during the trial, though some plants presented averages ranging between 700 and 600 in November-2013. Estimated Y-values of *L. scoparium* seedlings decreased in the second summer compared to the first (Y-value in Jan.13 = 771.8, Y-value in Jan.14 = 732.1), contrarily to the averages of *O. leptophyllus* seedlings, which were higher in January-2014 than in the January-2013 (Y-value in Jan.13 = 785.5, Y-value in Jan.14 = 797.3).

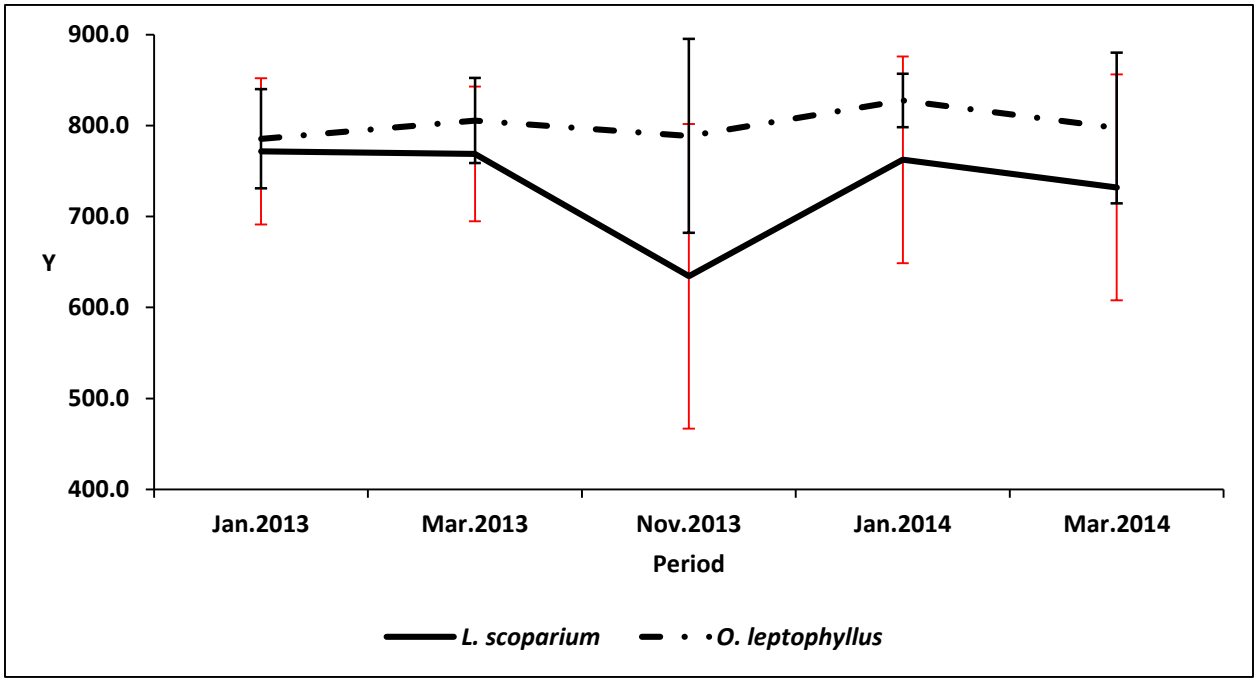


Figure 4-34 Average Y-values and respective 95% credible intervals of *Leptospermum scoparium* and *Ozothamnus leptophyllus* seedlings throughout the experiment period. Dierickx Farm.

Leptospermum scoparium

The results obtained for *L. scoparium* seedlings in January-2014 can only be presented for six treatments since all seedlings in the control plots were dead by then. Estimated Y-values in the second summer measurement were ≥ 703.1 (Figure 4-35). Average Y-values were higher in the H+S treatment than in the C-S ($P_{H+S|C-S} = 0.85$) and in the C+S ($P_{H+S|C+S} = 0.81$). Y-values in the M+S were also markedly higher than those in the C-S ($P_{M+S|C-S} = 0.83$) and C+S ($P_{M+S|C+S} = 0.80$). M+S and H+S had statistically equal effects on this parameter ($P_{M+S|H+S} = 0.50$). There were small statistical differences between H-S and H+S ($P_{H-S|H+S} = 0.58$), and between H-S and M+S ($P_{H-S|M+S} = 0.57$). Differences between estimated Y-values in the H+S and in the M-S may also be considered irrelevant ($P_{H+S|M-S} = 0.58$), as were the comparisons of estimated Y-values in the M+S and M-S ($P_{M+S|M-S} = 0.55$). C-S promoted higher estimated fluorescence readings than M-S ($P_{C-S|M-S} = 0.72$) and H-S ($P_{C-S|H-S} = 0.78$), and differences between H-S and M-S may be considered statistically irrelevant ($P_{H-S|M-S} = 0.48$; Table 4-30).

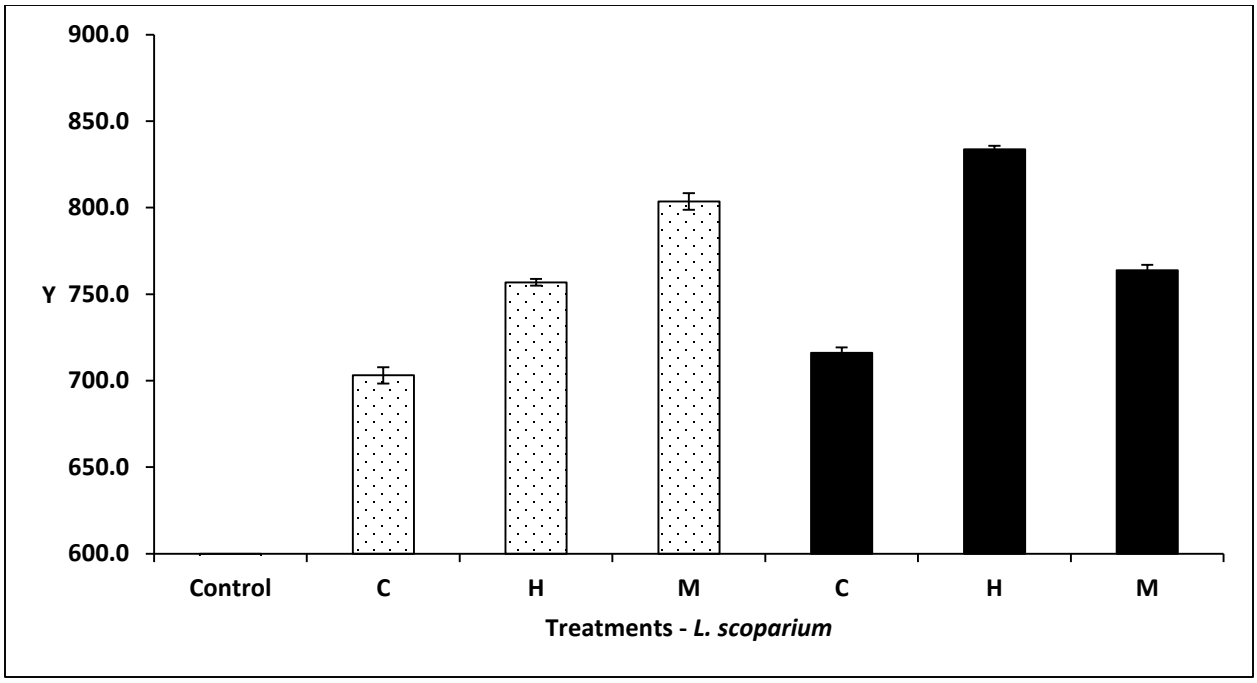


Figure 4-35 Estimated chlorophyll fluorescence readings and respective 95% credible intervals of *Leptospermum scoparium* seedlings in January-2014, per treatment. Dierickx Farm.

Table 4-30 Comparison of estimated Y-values of *Leptospermum scoparium* seedlings among treatments for January-2014. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(Y_A > Y_B|\text{data})$, where Y refers to estimated chlorophyll fluorescence. Dierickx Farm.

Treatment	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
C-S	0					
H-S	0.78	0				
M-S	0.72	0.48	0			
C+S	0.60	0.25	0.33	0		
H+S	0.85	0.58	0.58	0.81	0	
M+S	0.83	0.57	0.55	0.80	0.50	0

Ozothamnus leptophyllus

Average Y-values of *O. leptophyllus* seedlings in January-2014 ranged from 726.1 (H-S) to 883.1 (C+S), and they were more elevated in the shaded treatments (Figure 4-36). There was a strong grass-removal-and-shade effect on fluorescence readings compared to control ($P \geq 0.92$), and seedlings in the grass-removal-only also presented higher estimated Y-values than control ($P \geq 0.76$). There were no statistically relevant differences among the shaded treatments ($P = 0.47 \sim 0.52$), or among the grass-removal-only treatments ($P = 0.40 \sim 0.60$). Estimated Y-values of *O. leptophyllus* seedlings in the H-S were statistically lower than those in the shaded treatments ($P_{C+S|H-S} = 0.76$, $P_{M+S|H-S} = 0.77$, $P_{H+S|H-S} = 0.79$). As for the other comparisons, differences may be considered small ($P = 0.66 \sim 0.69$, Table 4-31).

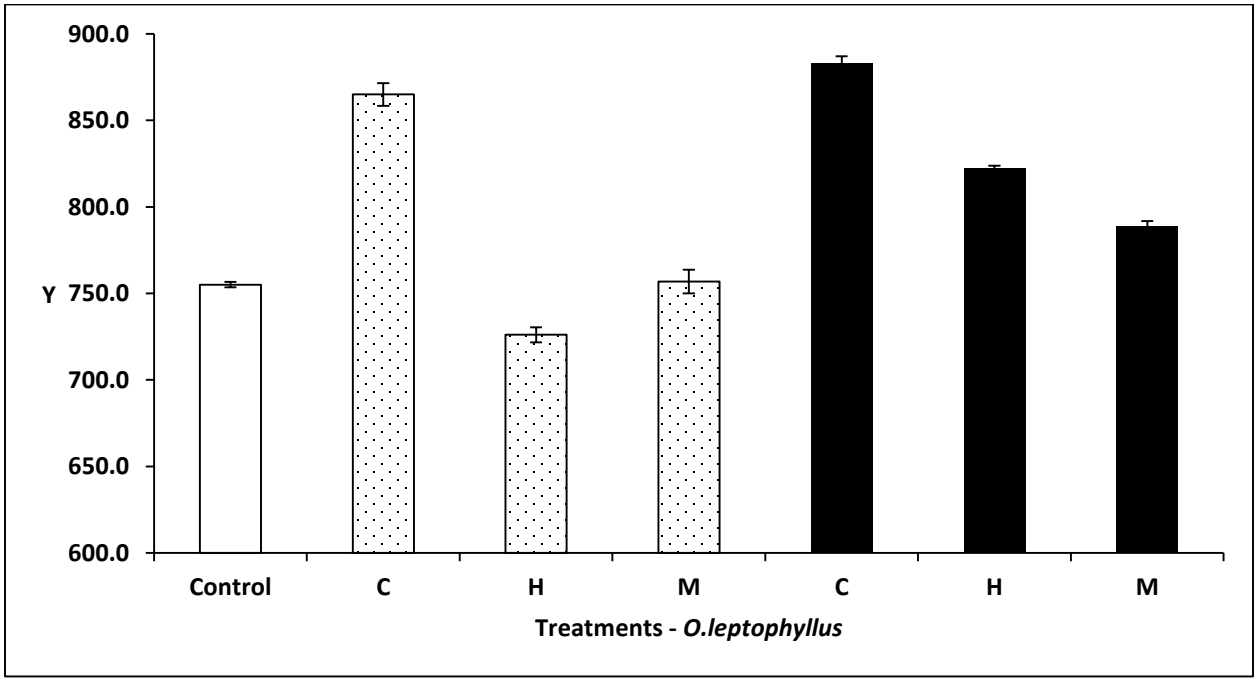


Figure 4-36 Estimated chlorophyll fluorescence readings and respective 95% credible intervals of *Ozothamnus leptophyllus* seedlings in January-2014, per treatment. Dierickx Farm.

Table 4-31 Comparison of estimated chlorophyll fluorescence readings of *Ozothamnus leptophyllus* among treatments seedlings in January-2014. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(Y_A > Y_B|\text{data})$, where Y refers to estimated chlorophyll fluorescence. Dierickx Farm.

Treatment	**Control**	**C-S**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0						
C-S	0.83	0					
H-S	0.76	0.40	0				
M-S	0.81	0.50	0.60	0			
C+S	0.93	0.69	0.76	0.66	0		
H+S	0.93	0.70	0.79	0.69	0.52	0	
M+S	0.92	0.67	0.77	0.66	0.49	0.47	0

4.3.5 Carbon Isotope Analysis - $\delta^{13}C$

Statistical analyses of carbon isotopic signature of *L. scoparium* seedlings were only performed for six out of the seven treatments originally established at Dierickx Farm because there were no seedlings left in the control plots when leaf samples were collected. Estimated $\delta^{13}C$ values (Figure 4-37) ranged from -26.03‰ to -28.81‰, and statistical comparisons presented in Table 4-32 show no distinct differences in averages among treatments (P = 0.35 ~ 0.69). Estimated $\delta^{13}C$ values of *O. leptophyllus* seedlings ranged from -27.92‰ to -30.95‰ (Figure 4-38). Averages were statistically more negative in the M+S compared to H-S ($P_{M+S|H-S}$ = 0.71). As for the remaining treatments, differences in estimated $\delta^{13}C$ values (P = 0.39 ~ 0.66) may be considered inexpressive (Table 4-33).

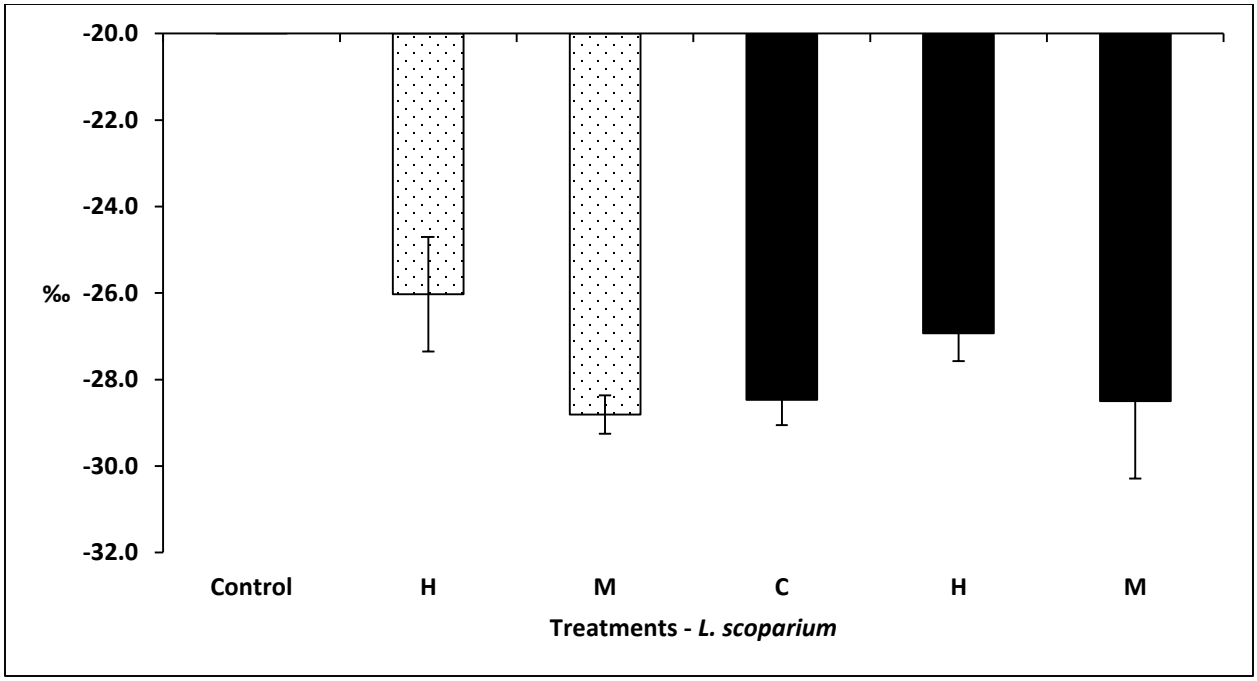


Figure 4-37 Estimated $\delta^{13}C$ values and respective 95% credible intervals for *Leptospermum scoparium* seedlings per treatment: Pattern fill – grass removal and no-shade treatments. Solid fill – grass removal and shade treatments. Dierickx Farm.

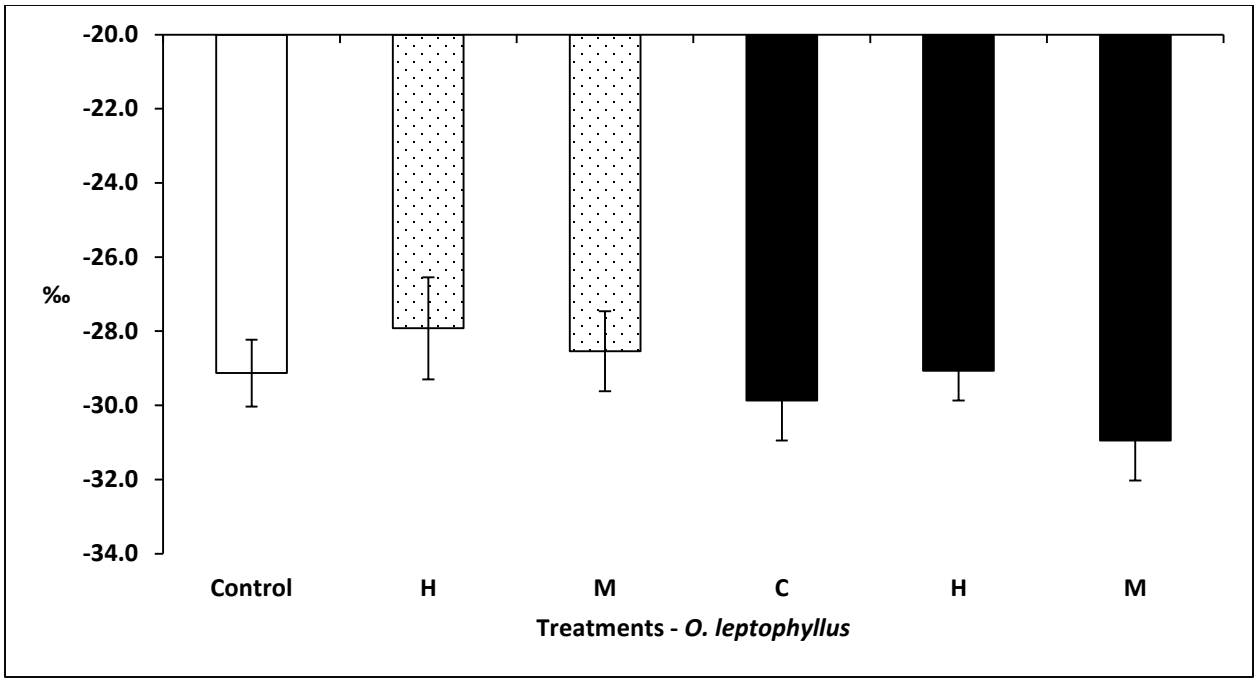


Figure 4-38 Estimated $\delta^{13}C$ values and respective 95% credible intervals for *Ozothamnus leptophyllus* seedlings per treatment: Pattern fill – grass removal and no-shade treatments. Solid fill – grass removal and shade treatments. Dierickx Farm.

Table 4-32 Comparison of estimated $\delta^{13}C$ values of *Leptospermum scoparium* seedlings among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\delta_A > \delta_B|data)$, where δ refers to estimated $\delta^{13}C$ values. Dierickx Farm.

Treatment	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
H-S	0				
M-S	0.69	0			
C+S	0.69	0.48	0		
H+S	0.55	0.35	0.38	0	
M+S	0.69	0.50	0.49	0.64	0

Table 4-33 Comparison of estimated $\delta^{13}C$ values of *Ozothamnus leptophyllus* seedlings among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\delta_A > \delta_B|data)$, where δ refers to estimated $\delta^{13}C$ values. Dierickx Farm.

Treatment	**Control**	**H-S**	**M-S**	**C+S**	**H+S**	**M+S**
Control	0					
H-S	0.39	0				
M-S	0.42	0.55	0			
C+S	0.53	0.66	0.61	0		
H+S	0.48	0.57	0.54	0.45	0	
M+S	0.60	0.71	0.65	0.55	0.61	0

4.4 Discussion

4.4.1 Effects of Shade

Overall, *Kunzea robusta*, *Pittosporum tenuifolium*, *Leptospermum scoparium* and *Ozothamnus leptophyllus* seedlings at the Rank Grass sites had the highest probability of survival and growth in the shaded treatments. The results concur with other studies showing that either natural or artificial shade can be crucial for transplanted native seedlings to grow in degraded areas (Hammond, 1995), especially in arid or semi-arid landscapes similar to New Zealand's dryland zone (Maestre et al., 2001; Benayas et al., 2005; Payne & Norton, 2011). Cortina and Maestre (2005) identified in half of the studies on plant effects on soil moisture in drylands that shade was mentioned as an important driver of positive plant survival and growth. The positive relationship found between shade and seedling establishment was probably linked to increased soil moisture under these treatments. Shade is noted to impact soil moisture by influencing soil water balance (Cortina & Maestre, 2005). In a dryland area in Hawaii, Cabin et al. (2002) identified that in exposed conditions, shade promoted a more benign microenvironment associated with reduced light levels and lower air and soil temperatures; consequently, soil water levels tended to increase (McLaren & McDonald, 2003). Soil moisture was the key determinant of plant productivity in temperate grasslands (Flanagan et al., 2002) and other ecosystems that present high inter-annual precipitation variability (Yuan et al., 2009). In such environments, higher soil water content is capable of counteracting the detrimental effects of direct sunlight and high temperatures on plants, thus increasing the probability of seedling survival (Chaves et al., 2002; Yang et al., 2005).

The four native woody seedlings planted at the Rank Grass sites had highest growth rates under the shade cloths, which provided a shade factor of 25-35%. Veenendaal et al. (1996) compared seedling growth of 15 West African tree species at five irradiance levels, and found that most tree species attained maximal growth rates at 20-50% irradiance or intermediate light conditions. Irradiance levels probably affected biomass production of the native seedlings at the Rank Grass sites as differences between relative height increment of plants growing in the unshaded and shaded treatments were substantial. The species used in this research were selected for possessing pioneer-like characteristics (Esler & Astridge, 1974; Allen et al., 1992; Mackay et

al., 2002; Dawson et al., 2011) which, among other features, are expected to be more tolerant to drier or well-drained soils and exposure to direct sunlight (Stephens et al., 2005). However, plant development is impacted because soil moisture becomes a limiting resource as light availability (Bunker & Carson, 2005) and temperatures rise (Chaves et al., 2002; de Gouvenain et al., 2007). The negative effects of limited soil water can be even more sever in fast-growing pioneer species that typically sacrifice water use efficiency to maximize growth (Poorter, 2005; Engelbrecht et al., 2006).

The native seedlings that survived in the control and unshaded treatments could have invested more in root growth to the detriment of stem elongation as a protective measure from direct sun light and other undesirable environmental conditions related to high light (Poorter, 1999). Seedlings can develop longer root systems to exploit deeper soil water sources (Letts et al., 2010) when growing in extreme light and temperature environments (Ballaré et al., 1996; Furness et al., 2005). Although root biomass was not measured in this experiment as the plants needed to be left in the ground for restoration purposes, it is possible that the surviving seedlings in the unshaded and control plots may have developed deeper root systems to go below the root zone of exotic grasses where soil moisture is rapidly reduced (Clary et al., 2004) and explore water and nutrient within lower soil layers (Letts et al., 2010). More root elongation resulting in reduced stem growth in the first years of seedling establishment is a characteristic often observed in plant species of arid and semi-arid ecosystems (Letts et al. 2010; Castro and Kauffman 1998; Silva 2003), and it is not an uncommon trait in New Zealand species (Bee et al., 2007).

The shade cloths could also have worked as physical barriers and protected the native seedlings growing at the Rank Grass sites from adverse weather elements, such as strong winds, frost and snowfall (Figure 4-39). Extreme weather conditions are common to the Lake Tekapo region, and high winds could have heightened soil water deficit and the desiccation effects of direct solar radiation on the native seedlings planted on Dierickx Farm. Caldwell (1970) found that transpiration and photosynthesis decreased with increasing wind speed (from 0.5 m/s to 8 m/s or 1.8 km/h to 28.8 km/h) due to full or partial closure of stomata in *Pinus cembra* and *Rhododendron ferrugineum*. Lake Tekapo region experienced high wind speeds throughout most of the experimental period, with average peak readings in the summer (highest monthly average

recorded = 5.5 m/s or 19.8 km/h in January-2014), when soil water content in the Dierickx Farm trail was also at its lowest. Average wind speed on fair summer days have been recorded to reach up to 13 m/s (46.8 km/h) in an experiment conducted by Kossmann et al. (2002) in the Takepo region. Strong wind fields can occur in mountainous areas such as the Mackenzie Basin due to differences in surface types and the presence of water bodies and glaciers that generate multiple and interacting thermally induced circulation systems, from small scale slope flows and lake breezes, to along-valley wind systems and mesoscale plain-to-basin circulations (Kossmann et al., 2002). Therefore, the shelter created by the shade cloths was probably crucial in protecting *L. scoparium* and *O. leptophyllus* seedlings from the high wind speeds common to the site (Figure 4-40), besides the aforementioned benefits related to improved microclimate and soil moisture. In winter, the shade cloths likely shielded the seedlings from the mechanical damage of the heavy snowfall (Körner 1998). Additionally, the shade cloths may have protected the seedlings during snowless winter days when extremely low air and soil temperatures, and frost can occur (Krause & Weis, 1991; Körner, 1998; Inouye, 2000).

Frost can occur during winter in Northern Canterbury if there are temperature inversions close to the ground surface (Gallo et al., 2014), although this phenomenon is not as common as in the Mackenzie Basin. In the case of Tiromoana Bush and The Willows Reserve, most seedling mortality occurred during summer likely as a consequence of elevated temperatures and irradiance in these areas. Nevertheless, some of the dieback that occurred between April and October-2013 (autumn and winter) could be related to damages to and desiccation of leaves caused by frost heaving and/or extremely cold temperatures (Körner 1998; Inouye 2000). Frost occurs when rapid declines in temperature take place because of radiation inversion in the nighttime, with accumulation of cold air at lower altitudes, creating “cold-air pools” (Vosper & Brown, 2008). The decrease in average seedling height over autumn and winter was more accentuated in the unshaded and control treatments at Tiromoana Bush and Willows Reserve sites, similarly to what was detected at Dierickx Farm. Matusick et al. (2014) found that canopy damage and dieback on *Eucalyptus marginata* and *Corymbia calophylla* trees in the Mediterranean climate region of southwest Australia were widespread and strongly correlated to when cold-air pooling formed in valleys and lower to mid-slope position (projected minimum air temperatures ranged from -0.1 to -2.7 C at valley bottom). The results obtained in the Rank

Grass trials could be an indication that, without the shade cloths, native seedlings are also vulnerable to the cold temperatures and frost in the Northern Canterbury dryland areas.

Figure 4-39 Damages to the shade cloth plots at Dierickx Farm likely due to heavy snowfall and strong winds during the winter of 2013. Photo taken on 06th of October, 2013.

Figure 4-40 One *Leptospermum scoparium* seedling (M-S plot) with main stem broken at the base probably caused by snowfall or high wind during winter. Dierickx Farm Photo taken on 06th of October, 2013.

4.4.2 Effects of Grass Removal

The establishment and development of the native seedlings on the Rank Grass sites was largely affected by the grass removal methods, although at varying degrees and depending on the presence or absence of shade cloths. Stevenson and Smale (2005) found that the seedlings of two native woody species, *Kunzea ericoides* and *Coprosma robusta*, would only establish on a pastoral ecosystem in Hamilton, New Zealand, after different grass removal methods were implemented, likely for reducing competition with exotic grasses and increasing soil water availability. Grass removal opened a gap within an exotic tamarisk weed canopy (*Tamarix* spp.) in northwestern Colorado and resulted in increased light reaching cottonwood seedlings and reduced transpiration area, consequently increasing seedling survival possibly due to more elevated soil water availability (Cooper et al., 1999).

Cultivation was the one grass removal method that, statistically, resulted in the highest survival and growth responses for all four native seedling species at the three Rank Grass sites. Stevenson and Smale (2005) tested several ground treatments on native plant species germination and seedling establishment on a pastoral landscape in Hamilton, New Zealand, and found that, after one year, the majority of the native *Kunzea ericoides* and *Coprosma robusta* seedlings had higher survival rates on the topsoil-removed treatment (grass cover and topsoil layer removed to approximately 10 cm deep), which likely has a similar effect to the cultivation treatment described here. The results obtained in the Rank Grass experiments may be related to the type of cultivation method used termed in the literature as "conservation cultivation or tillage" (Mannering et al., 1987). This type of management system turns over the soil surface and leaves plant residue covering about 30% of the surface (Page et al., 2013) and, over a short time, decreases soil bulk density and increases soil macro-porosity, or aeration (Özgöz, 2009). Plants can develop more fully in well-aerated soils because of higher water infiltration and storage (Page et al., 2013). Plants can also benefit from reduced soil organic carbon loss and replenished soil fertility among other improved soil physical properties linked to conservation tillage (Das et al., 2014). The higher seedling survival and growth in the cultivation treatments at the Rank Grass sites can also be a result of reduced root competition with exotic grasses where the soil surface was disturbed by cultivation. Competition for belowground resources can cause failure of tree seedling establishment and be a significant constraint for seedlings establishment in natural

and semi-natural plant communities (Coomes & Grubb, 2000) just as a harsh microclimate of an exposed human-induced grassland environment can (Gunaratne et al., 2011).

Herbicide application at the Rank Grass sites resulted in some positive responses from the native seedlings as well. Controlling exotic herbaceous species with herbicides on former agricultural lands, which normally have higher soil fertility levels than under natural circumstances, has been proven to be effective for transplanted seedlings in many instances (D'Antonio & Meyerson, 2002; Sweeney et al., 2002; Burrows et al., 2015). Presumably, the temporary reduction of the dominant grass after spraying herbicide on the respective plots on the Rank Grass sites led to an increase in available resources, such as water and soil organic carbon (Syrett et al., 2012), by eliminating competition with the exotic grasses, thus stimulating native seedling growth (Davis & Pelsor, 2001; Peltzer & Köchy, 2001). However, herbicide was generally more effective when combined with shade, likely due to the collective positive effects of increased soil fertility following herbicide application (Syrett et al., 2012) and the effects of shade on hydrological processes, such as soil water levels, as previously discussed (Redding et al., 2008). Additionally, shade influences ecosystem functions such as nutrient cycling (Royer et al., 2011), by protecting the soil's microbial communities from high irradiance, which have an important role in litter decomposition; hence, influencing plant development (Caldwell et al., 2007). Therefore, the native seedlings at the Rank Grass sites in the H+S treatment had better survival and growth rates than those in the H-S plots because of the additional and positive effect of shade on the nutrient release of the dying grasses and weeds immediately after the application of the herbicide, besides the improved microclimate and higher soil water levels.

Herbicide application may have had a disadvantage, however, as the immediately availability of resources that followed the death of the grass cover after spraying could have favored the growth of opportunistic exotic plant species, such as clover at The Willows Reserve, and California thistle at Tiromoana Bush (Stevenson and Smale 2005). Glyphosate, the contact herbicide used in this research, provided temporary relief for the native seedlings, but exotic plant species quickly re-colonized the plots a few months later. Davis & Pelsor (2001) demonstrated that a resource surge after the initial dieback from herbicide application probably led to increased invasion success in Minnesota grasslands up to 1 year after the application of glyphosate. An

environment tends to be more susceptible to invasion following an abrupt increase in the rate of supply, or a decline in the rate of uptake, of a limiting resource (Walker et al., 2005). It is likely that the native seedlings on the Rank Grass sites will be outcompeted by the exotic plant species in the long term after herbicide application has been discontinued, since the tendency is for the native species cover to decrease as exotic weed and grass densities remain the same (Walker et al., 2005).

Mulch was more significant in maintaining the highest soil water levels on all three Rank Grass sites, even in the absence of shade. Mulch has been described as an effective treatment in rising soil moisture levels because it reduces direct incidence of solar radiation and corresponding soil desiccation (Winkel et al., 1991; Romic et al., 2003). Mulches are well known for modifying the energy and water balance at the surface of soils and creating more favorable conditions for plant growth (Farias-Larios et al., 1994; Romic et al., 2003). In addition, where water is very restricted, and irrigation is not an option, mulch is commonly used as a water-saving tool for crop production. Nevertheless, the native seedlings in the Rank Grass experiments did not perform as expected in the mulched plots, unless shade was included. Sweeney et al. (2002) found that tree mat (another type of mulching) resulted in survivorship rates greater than 50% after 4 years only when combined with tree shelter for *Quercus palustris* (pink oak), *Q. rubra* (red oak), *Q. alba* (white oak), *Betula nigra* (river birch), and *Acer rubrum* (red maple) at two riparian sites in Maryland, USA. The responses to M+S also seemed to vary among species. *K. robusta* and *P. tenuifolium* seedlings had high survival and growth rates in the M+S plots at Tiromoana Bush and The Willows Reserve sites. The same results were observed for *L. scoparium* seedlings but not for *O. leptophyllus* seedlings on Dierickx Farm, in the Mackenzie Basin. Stevenson and Smale (2005) also found that mulching had variable effects on *K. ericoides* and *C. robusta* germination and seedling development. The mulch used for the Rank Grass experiments was effective in elevating soil moisture, as explained previously, but also in smothering the exotic grass cover and preventing recolonization of the plots probably by trapping solar heat below the plastic cover, thus killing weed and grass propagules on the soil surface (Elmore et al., 1997; Melander & Jørgensen, 2005). However, some grass and weed still managed to emerge through the holes in the mat where the native seedlings were growing. Though mulching was successful in preventing annual grass germination on an abandoned

farmland in California, it did not reduce annual exotic forbs emergence that were the dominant species in the plots (Marushia & Allen, 2011).

Native seedling survival and growth rates were extremely low in the mulch-no-shade (M-S) treatment, even though soil moisture levels under this treatment were expressively high. The mulch treatment used in the Rank Grass trials had a layer of organic material (coconut fiber) covering the black plastic mat in order to decrease evaporation from soil surface and increase infiltration by slowing surface water movement (Winkel et al., 1991; Montalvo et al., 2002). In the western U.S., protection from wind and water erosion for fragile soils and young seedlings is commonly accomplished with organic mulches that add organic matter to the soil, lower surface temperatures, and retain moisture (Anderson & Ostler, 2002). However, the coconut fiber and black plastic mats used on the Rank Grass sites did not have the expected advantageous effects on seedling establishment under unshaded conditions. The coconut fiber cover did not avoid desiccation of seedlings in the M-S treatment, a typical sign of difference in microclimate between the cooler, shaded and more humid conditions inside the mulch and the exposed conditions outside (Stevenson and Smale 2005). Organic mulch (forest floor) had no beneficial effect on *Kunzea ericoides* and *Coprosma robusta* seedlings growing on a pastoral area in New Zealand's North Island (Stevenson and Smale 2005). The thermal trap created by the black plastic mat may have been responsible for the adverse response of the native seedlings to the M-S treatment (Marushia & Allen, 2011), that somehow cancelled out, or minimized, the supposedly beneficial effects of the organic layer. Black plastic used for solarization[2] is not effective on dry soils since this technique relies on soil water to conduct heat (Elmore et al., 1997; Melander & Jørgensen, 2005). Solarization has been reported to limit restoration of native vegetation in Mediterranean-like climates or in cool-climate regions where temperatures are not consistently warm for long enough periods to raise temperatures under the plastic mulch (Marushia and Allen 2011). Ideally, it would have been used a purely organic mulch, such as bark chips or the coconut fiber mat only, as the mulch treatment on the Rank Grass sites, but this

[2] Solarization, or solar heat sterilization, is a common method used in restoration projects and landscaping to smother and kill unwanted grass and weed seeds, plants, and pathogens on surface of the soil. The process involves the use of a plastic mat covering the ground, thus trapping heat underneath generated by solar radiation. Elmore CL, Stapleton JJ, Bell CE, and Devay JE. (1997) Soil solarization: a method for controlling diseases, nematodes and weeds. University of California, California, USA

was not possible because of the frequently adverse weather conditions, specially strong winds, that would have likely destroyed the mulch cover. Use of a purely organic mulch may well have resulted in different outcomes for the seedlings.

As stated earlier, soil moisture levels were markedly higher in the mulched treatments at the Rank Grass sites, even in the absence of shade. Seedling mortality and low growth rates in the M-S plots could also be related to the negative effects of plastic mulch on non-uniform distribution of water, a frequent feature of former agricultural or pastoral lands with compacted soils (Yates et al., 2000). In these situations, the plastic mulch can intensify the potential accumulation of water in the root zone and provoke plant mortality by anoxia (Romic et al., 2008). Anoxia is frequent on compacted soils due to their poor soil drainage capacity (Pfeifer et al., 2014). The effect of mulch in elevating soil temperature underneath it stimulates the microorganism respiration, and plant roots experience a transition from a fully aerobic to anaerobic environment in less than 24 hours due to complete depletion of O_2 (Erdmann & Wiedenroth, 1988; Good & Paetkau, 1992; Crawford, 2012).

Another important observation is that soil moisture levels in the cultivation and herbicide treatments were not statistically different in the absence of shade. Additionally, at times, soil water levels in the control plots were higher than in the H-S or C-S at two out of three study sites (The Willows Reserve and Dierickx Farm). Cultivation and herbicide application were pointed out as having caused a decrease in soil moisture in a sub-montane woodland area (D'Antonio et al., 1998). A similar pattern was registered in dry pastures in Panama, where grass removal caused either a decrease or no change in soil moisture (Griscom et al., 2005). Litton et al. (2008) detected no significant changes in soil water levels following grass removal in a dry forest in Hawaii. Nevertheless, native seedling establishment and growth at the Rank Grass sites were more pronounced when the exotic grass cover was removed, similarly to the findings of Riginos (2009) who detected the positive height relationship and grass removal of *Acacia drepanolobium* trees in Kenya. The results of the Rank Grass sites may also indicate that native seedling establishment may not be entirely reliant on soil moisture, but rather on the combined effects of grass removal and shade. February et al. (2013b) manipulated precipitation levels and tested grass removal effect on tree growth in a semi-arid savanna area of the Kruger National Park in

South Africa and observed that plants responded more significantly to grass removal than to increased soil moisture. Trees are poorer competitors for soil water than grasses, and do not necessarily benefit from increases in soil moisture if grasses are still present (Kulmatiski & Beard, 2013). Increases in soil moisture led to increases in grass root biomass, which in turn increased the transpirational demand of grasses, reducing the water potential gradient from the soil to grass roots and effectively made this resource less available to trees (February et al., 2013b). Therefore, the removal of the grass cover can benefit native tree seedlings not by increasing soil moisture, as higher soil water levels do not necessarily imply more water availability to plants, but by reducing root competition with grasses for soil resources as suggested by February et al. (2013a).

4.4.3 Measurements of Stress

Chlorophyll fluorescence readings of the native seedlings planted on the three Rank Grass sites presented a similar pattern of fluctuation along with the seasons and average soil moisture levels. Seedlings showed, on average, higher Y-values in the summer, when soil moisture was lowest, and lower Y-values in the cool seasons, when both precipitation and soil moisture were higher. Seasonal patterns in photosynthetic rates are common to most plants in regions with marked seasons, or defined rainy and dry periods throughout the year (Faria et al., 1996; Faria et al., 1998; Letts et al., 2010). Estimated Y-values and carbon isotope signature of the native seedlings under all seven treatments at the Rank Grass sites were within the indicative range for healthy, unstressed plants, with functionally efficient photosynthetic capacities (Griffiths, 1991). However, the growth and survival data suggested otherwise. The average Y-values and $\delta^{13}C$ of seedlings specifically in the unshaded and control treatments, where mortality and dieback rates were higher, could, in fact, have masked the actual water stress state of these seedlings. Increased stomatal conductance to overcome reduced photosynthesis under stress conditions leads to relative increases in water content, but also to higher carbon assimilation in order to improve the probability of the plant to persist in the environment (Padilla et al., 2009). Consequently, intracellular ^{13}C:^{12}C ratio increases (Chaves et al., 2002). Estimated $\delta^{13}C$ values also tended to be more negative in the shaded treatments, which was expected since low irradiance promotes better stomatal conductance, thus increasing the concentration of intercellular CO_2 and isotopic composition of leaves (Farquhar et al., 1989b).

Although average Y-values of seedlings in the unshaded treatments were ≥ 600 (with a few exceptions in early spring), they were generally lower than those of the shaded treatments. Except for *L. scoparium* seedlings at Dierickx Farm, estimated Y-values in the M-S treatment, in particular, were markedly lower than in all the other treatments, including control. Photoinhibition is another defense mechanism known to be triggered inside plants when under chronic or dynamic (moderate) environmental stress. Reduced stomatal conductance limits CO_2 fixation to balance CO_2 usage by the Calvin cycle under lower CO_2 production (Chaves et al., 2009). Protection mechanisms usually compete with photochemistry for the absorbed energy, leading to a decrease in quantum yield of photosystem II (Genty et al., 1989). However, plants can develop paraheliotropism to prevent photo-oxidative damage to leaf cells by producing protective compounds (anthocyanins) that mask chlorophyll similarly to "sunscreen" (Ryan & Hunt, 2005; Karageorgou & Manetas, 2006) and help dissipate the excessive energy in the cells through heat at the same time it guarantees efficient nutrient retrieval from senescing leaves to the storage compartments of the plant (Adams III et al., 2006). The other part of the excessive energy load in the cells is supposed to go to "quenchers" in the photosystem II reaction center (Cleland et al., 1986) that act as energy traps to allow fluorescence levels to remain low at Fo (minimal fluorescence, Butler 1978), but still within the photosynthetically efficient range (Krause & Weis, 1991).

The use of defense mechanisms to dissipate excessive energy due to high irradiance and temperatures, to maintain CO_2 levels in the leaves under water stress, and to invest in protective compounds to avoid or reduce photo-oxidative damages to the aboveground plant structures can help improve the chances of the seedling's persistence in harsh environments. Nevertheless, these mechanisms come at a cost for the development of plants (Baltzer et al., 2005). Plants under stress usually develop smaller stems and leaves, a trait often associated with lower photosynthetic nutrient-use efficiency (PNUE) due to increased nitrogen allocation to non-photosynthetic functions to produce defensive compounds and maintain greater water use efficiency (Terwilliger et al., 2001). Lower PNUE, inevitably, has a negative impact on a plant's respiration and, consequently, its development (Baltzer et al., 2005). Higher metabolic rates to compensate for the increased resistance to CO_2 diffusion due to stomatal closure (Reddy et al., 2004) and for biomass reallocation (Heilmeier et al., 1997) affect growth of plants in adverse

environmental conditions (Caldwell et al., 1998). Therefore, it is possible that the native seedlings planted in the control and unshaded treatments at the Rank Grass sites invested in protective mechanisms in order to survive even though it meant compromising their growth rates (de Gouvenain et al., 2007).

5. Results - Degraded Short Tussock sites

5.1 Weather Data – Mackenzie Basin

Total precipitation was 843.2 mm in Lake Tekapo region during the experimental period (Table 5-1), with monthly averages equal to 49.6 mm, but most of the rain fell in May and June-2013 (232.5 mm or 27.6% of the total amount of rain), with above average monthly rainfall events in January-2013 (101.9 mm or 12.1%) and October-2013 (82.95 mm or 9.8%). The 2013 calendar year received 667.2 mm or 79.1% of the total amount of rain for the entire period in which this experiment was carried out. The total amount of rain for 2013 was higher than the long-term average of 580.1 mm obtained from Lake Tekapo EWS and Lake Tekapo Air Safaris weather stations between 1994 and 2014 (https://www.niwa.co.nz). The lowest total monthly rainfall was registered in April-2013 (10.7 mm. Monthly average air temperatures varied between -3.2°C (June-2013) and 23.9 °C (February-2013), with a monthly average maximum air temperature of 16.6°C (Figure 5-1).

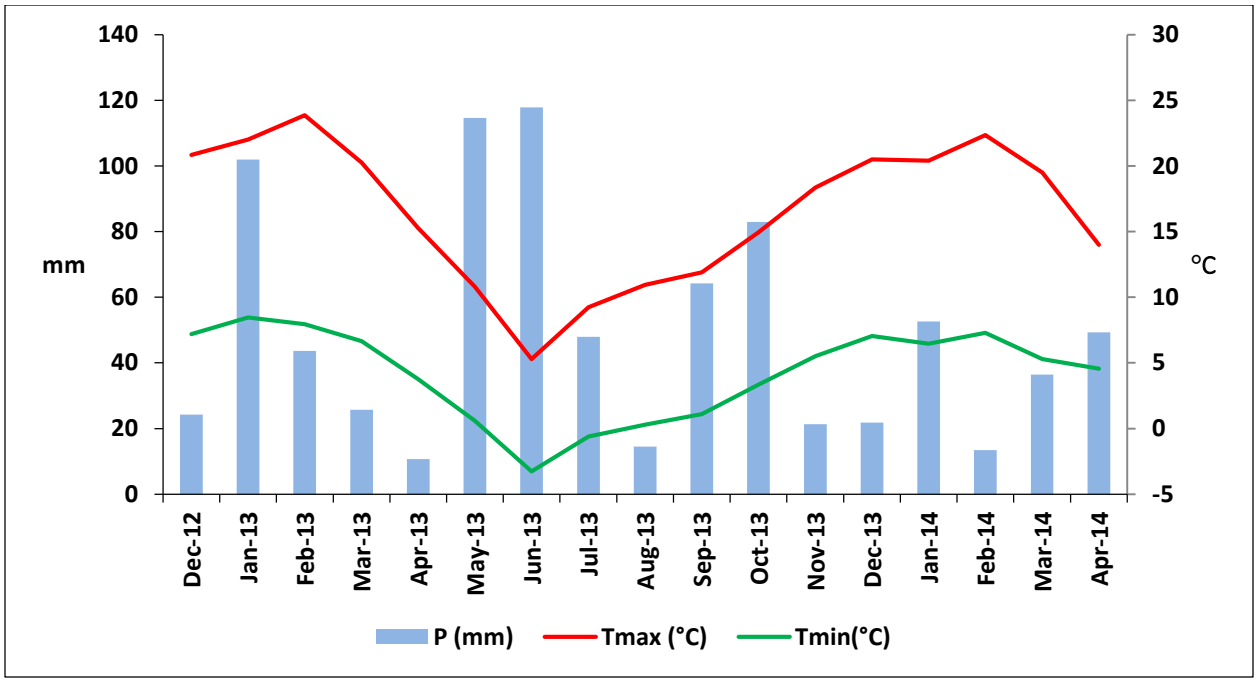


Figure 5-1 Monthly weather averages for Tekapo Region for the experimental period. Tmax – maximum air temperature, Tmin – minimum air temperature. Source: http://cliflo.niwa.co.nz.

Table 5-1 Averages, standard deviations, maximum and minimum values of the weather data for Lake Tekapo/Mackenzie for the experimental period (17 months) based on the data collected from Tekapo EWS and Lake Tekapo Air Safaris weather stations. Tmax – maximum air temperature; Tmin – minimum air temperature. Source: http://cliflo.niwa.co.nz).

Statistical Parameters	**Rain (mm)**	**Tmax (°C)**	**Tmin (°C)**
Average	49.6	16.5	4.2
sd	34.3	5.2	3.3
Max	117.9	23.9	8.5
Min	10.7	5.3	-3.25

5.2 Irrigation Trial

5.2.1 *Soil water content*

Overall, the results show that Θ fluctuated along with the seasons, and treatments reached the highest values recorded in the trial in October-2013 (Θ ≥ 36.8%), coincidently after and during two months with above the average monthly precipitation (September and October combined = 147.15 mm, see Figure 5-1). By the end of the experiment, averages had increased in the I-S+,I+S-, and I+S treatments (35.5%, 42.3%, and 44.3%, respectively), whereas Θ under the control plots was below 30%, similarly to the average recorded at planting. The first Θ analysis indicated that averages were homogenously distributed across the study site and ranged between 29.2% and 30.5%. The accumulated rainfall two weeks prior to transplanting the seedlings was 20.4 mm, but no rain was recorded on the day soil samples were collected (18/12/2012), or on any of the previous ten days that preceded the analysis. The highest average air temperature that day was 19.5°C, slightly above the average annual maximum air temperature for Tekapo (16.5°C), but relatively lower than the average maximum air temperature calculated for that month (20.85°C).

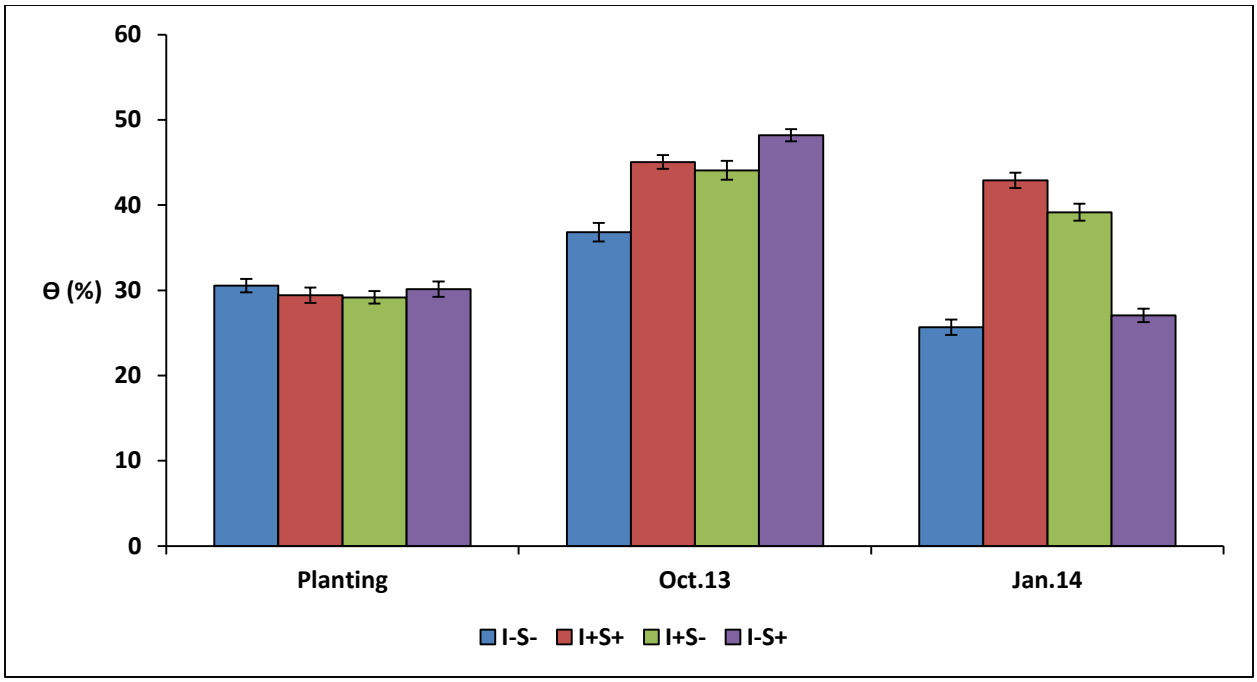


Figure 5-2 Estimated soil water content and respective 95% credible intervals per treatment at each monitoring period. Irrigation Trial.

Estimated Θ in the second summer (January-2014) was highest in the I+S+ treatment (42.8%), followed by the I+S- treatment (39.3%), while averages in the I-S+ and I-S- treatments remained below 30% (Figure 5-3). The average rainfall that month was 52.6 mm and more elevated than when the trials were established. Accumulated rainfall for the two weeks that preceded soil moisture monitoring was 27.2 mm, though no rain was recorded on the day soil samples were collected, nor on the previous five days. The average maximum air temperature on the day of Θ analysis was 25.3°C, higher than the average calculated for January-2014 (20.4°C) and at planting (19.5°C). Simulations in Table 5-2 indicate that supplemental water provided by irrigation promoted the markedly higher estimated Θ in January-2014 ($P \geq 0.88$). Although soil moisture under the I-S+ treatment was higher than under the control, differences were not statistically strong ($P_{I\text{-}S+|I\text{-}S-} = 0.56$).

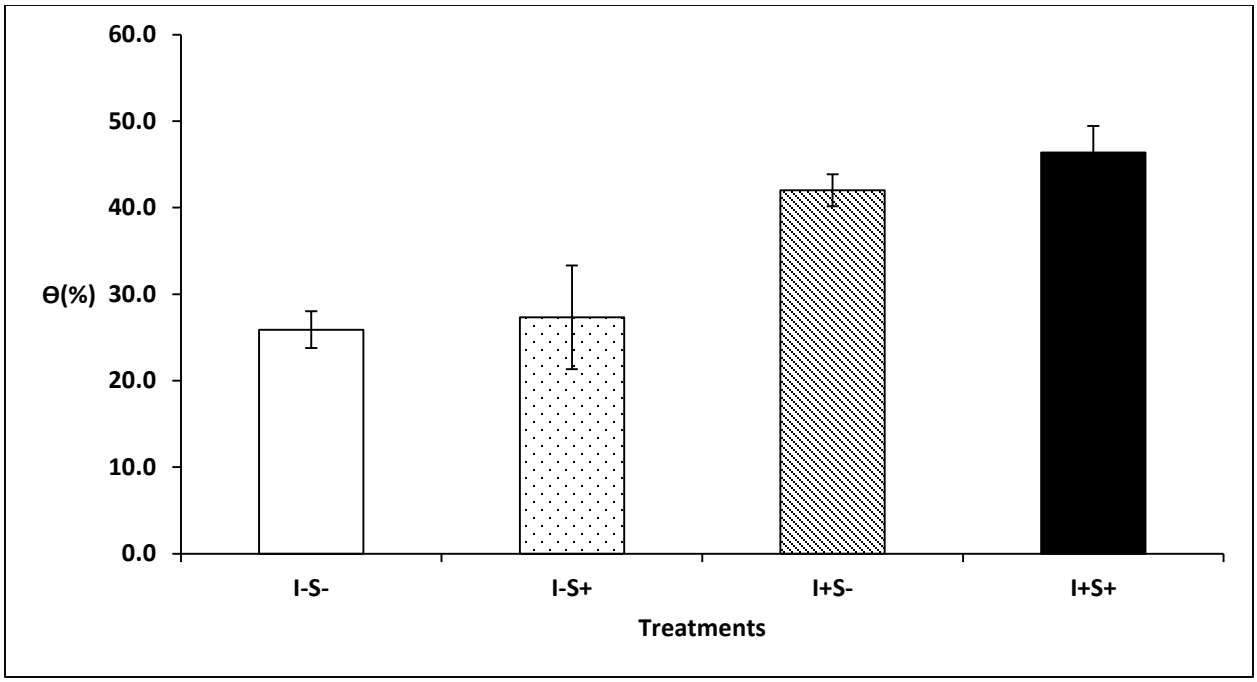


Figure 5-3 Estimated soil water content and respective 95% credible intervals for each treatment in January-2014. Irrigation Trial.

Table 5-2 Comparison of estimated Θ among treatments in January-2014. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\Theta_A > \Theta_B|data)$, where Θ refers to estimated soil water content. Irrigation Trial.

Treatment	**I-S-**	**I+S+**	**I+S-**	**I-S+**
I-S-	0			
I+S+	0.92	0		
I+S-	0.88	0.38	0	
I-S+	0.56	0.10	0.15	0

5.2.2 *Survival and Growth*

At the end of the experiment, 102 individuals of *Leptospermum scoparium* (70.8%) and 131 (91%) of *Ozothamnus leptophyllus* remained alive at the Glenmore Irrigation site. *L. scoparium* seedlings had the highest survival rate under irrigation and shade (I+S+), whereas *O. leptophyllus* had more survivors in the no irrigation-and-shade treatment (I-S+). Seedlings of both species had lowest number of survivors in the control plots (Table 5-3).

Table 5-3 Number of survivors of *Leptospermum scoparium* and *Ozothamnus leptophyllus* seedlings per treatment. Irrigation Trial.

Treatment	***L. scoparium***	***O. leptophyllus***
I-S- (control)	11	28
I+S+	32	34
I+S-	30	33
I-S+	29	36
Total	102	131

Leptospermum scoparium

The estimated probability of survival of *Leptospermum scoparium* seedlings was over 88% in all treatments except control (0.20; Figure 5-4A), which reflected on the marked treatment effect on this parameter compared to the control ($P \geq 0.99$). The combined effects of irrigation and shade (I+S+) on survival of *L. scoparium* seedlings was much higher than shade only ($P_{I+S+|I-S+} = 0.75$). Probability of survival in the I+S+ was also superior to irrigation only (I+S-), though differences were not statistically significant ($P_{I+S+|I+S-} = 0.68$; Table 5-4).

Mean heights of *L. scoparium* seedlings in the beginning of the trial ranged from 32.1 cm to 36.8 cm (Figure 5-5). Between planting and April-2013, mean heights of seedlings in the control (I-S-) and I+S+ treatments experienced dieback, while seedlings in the I+S- and I-S+ plots had an increase in average heights. During the cold seasons, from April to October-2013, seedlings had dieback and mean heights by October-2013 ranged from 15.1 cm (I-S-) to 33.7 cm (I+S+). Mean heights of *L. scoparium* seedlings continued to decrease in the following season and, by the end of the experiment in April-2014, mean heights ranged from 10.0 cm (I-S-) to 22.9 cm (I+S+). This ultimately reflected on the negative RHI values that this species showed in this trial (Figure 5-4B). The highest proportion of dieback was in the control plots (-1.3). Simulations in Figure 5-4 show that dieback was less intense in the I+S+ and I+S- treatments compared to the control ($P = 0.96$), and that these two treatments had relatively similar effects on *L. scoparium* seedling growth ($P = 0.53$). During the last measurement, many *L. scoparium* seedlings were observed to be re-sprouting (Figure 5-6). Although this data added to the overall number of survivors in this trial, it did not seem to have affected the average height curves, which show a continuous decline in all treatments.

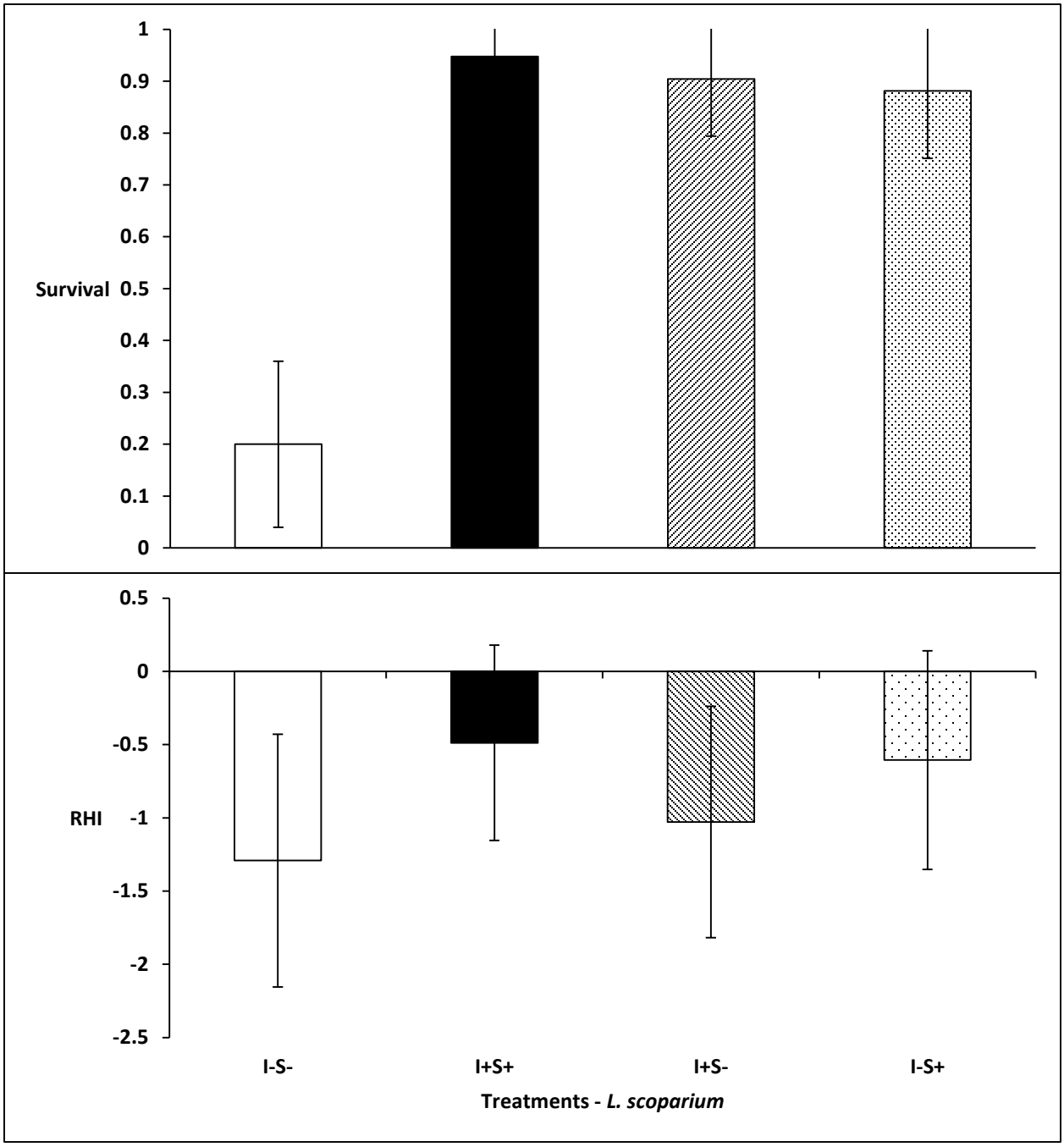


Figure 5-4 Estimated probabilities of survival (A) and Relative Height Increment (B), and respective 95% credible intervals, per treatment, for *Leptospermum scoparium* seedlings. Irrigation Trial.

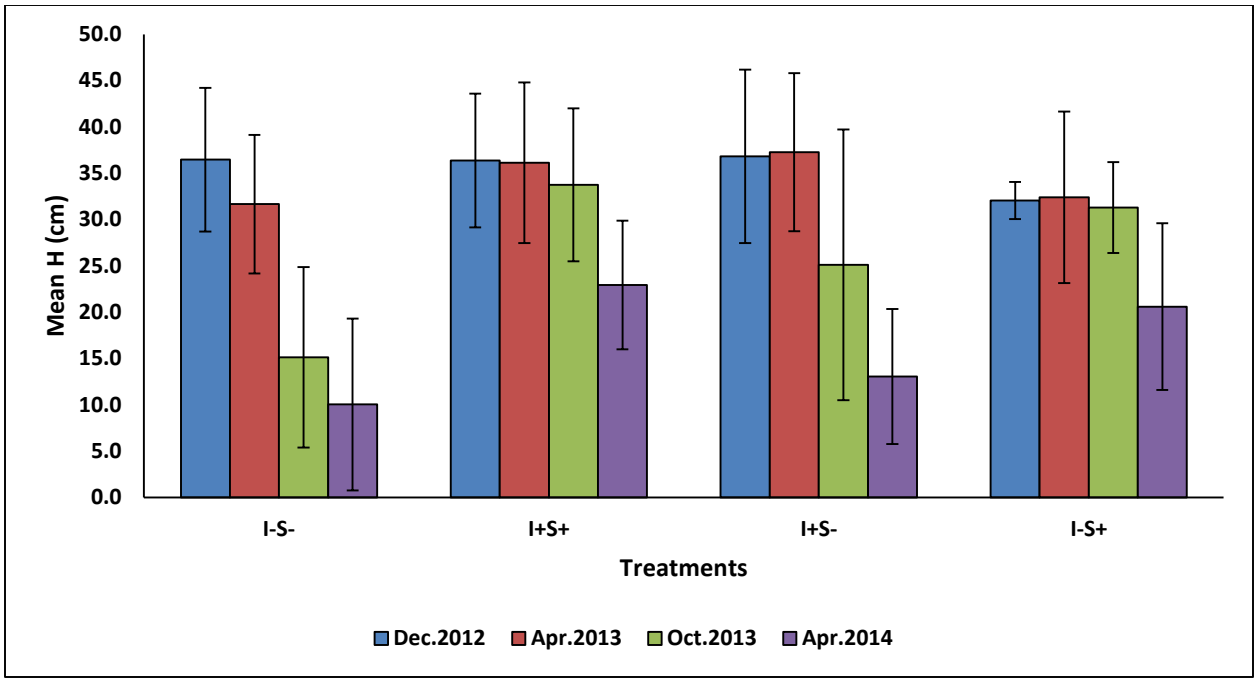


Figure 5-5 Mean heights (cm) of *Leptospermum scoparium* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. Irrigation Trial.

Table 5-4 Comparison of probability of survival among treatments for *Leptospermum scoparium* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(estS_A > estS_B|data)$, where estS refers to estimated probability of survival. Irrigation Trial.

Treatment	**I-S-**	**I+S+**	**I+S-**	**I-S+**
I-S-	0			
I+S+	0.99	0		
I+S-	0.99	0.32	0	
I-S+	0.99	0.25	0.42	0

Table 5-5 Comparison of RHI among treatments for *Leptospermum scoparium* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(RHI_A > RHI_B|data)$. Irrigation Trial.

Treatment	**I-S-**	**I+S**	**I+S-**	**I-S+**
I-S-	0			
I+S+	0.96	0		
I+S-	0.67	0.04	0	
I-S+	0.96	0.47	0.95	0

Figure 5-6 Two *Leptospermum scoparium* seedlings re-sprouting from the base of the plant. Main stem that had originally been used to measure plant height is completely dry and measurement in April-2014 was taken from the ground to the tip of the new green branch. Irrigation Trial.

Ozothamnus leptophyllus

Estimated probability of survival of *Ozothamnus leptophyllus* seedlings was over 81% in all treatments, including the control (Figure 5-7A). Seedlings had 100% probability of survival in the I-S+ treatment, followed by I+S+ (0.95). There was a strong treatment effect on *O. leptophyllus* seedling survival compared to the control ($P \geq 0.91$). Seedlings had higher survival under shade only (I-S+) than all other treatments in 100% of the simulations (Table 5-6

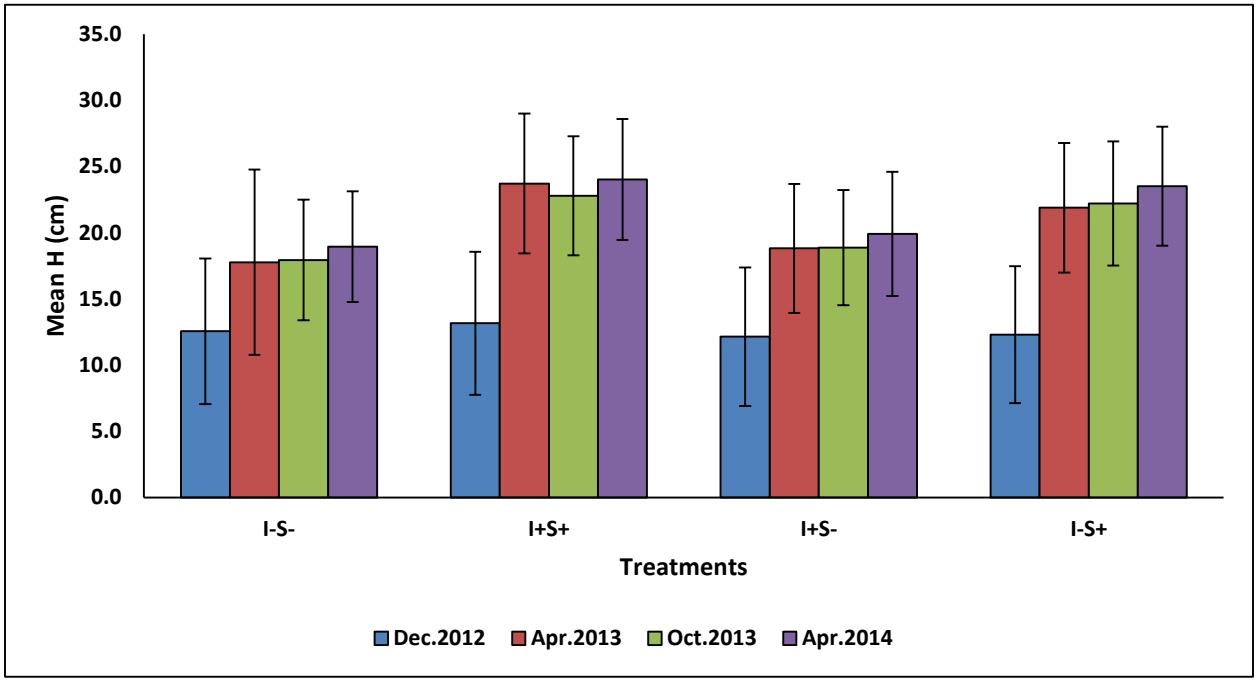


Figure 5-8 Mean heights (cm) of *Ozothamnus leptophyllus* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. Irrigation Trial.

Table 5-6). The combination of both treatments (I+S+) enhanced the probabilities compared to the control ($P_{I+S|I-S-} = 0.95$). Estimated probability of survival of *Ozothamnus leptophyllus* seedlings was also relatively greater in the I+S+ than in the I+S- ($P_{I+S+|I+S-} = 0.66$), although these differences may be considered small.

Mean heights of *O. leptophyllus* seedlings at the start of the trial ranged from 12.1 cm to 13.2 cm (Figure 5-8). Seedlings had an increase in mean heights during the first summer and in April-2013, seedlings had nearly doubled in size in the I+S+ and I-S+ treatments, and also had increased in size in the control (I-S-) and I+S-. Between April and October-2013, seedlings in the

I+S+ and I-S+ had dieback, whereas seedlings in the I-S- and I+S- had a small increase in average heights (< 0.5 cm increase, on average). Growth continued in the following period and, by the end of the trial, seedling mean heights ranged from 18.9 cm (I-S-) to 24.0 cm (I+S+). The increase in average heights of *O. leptophyllus* seedlings was detected in the positive RHI under all treatments (Figure 5-7B). Seedlings in the I+S+ plots experienced the highest RHI (0.75), whereas those in the I-S- plots had the lowest RHI. The results of the simulations in Table 5-6 show a strong I+S+ and I-S+ effect on seedling growth compared to the control ($P_{I+S+|I-S-} = 0.83$, $P_{I+S-|I-S-} = 0.77$). Seedling growth in the I+S- treatment, on the other hand, was not statistically different from the estimated growth rates in the control ($P_{I+S-|I-S-} = 0.55$). The combination of both treatments also promoted superior results to irrigation only ($P_{I+S+|I+S-} = 0.77$), and relatively similar effects compared to shade alone ($P_{I+S+|I-S+} = 0.57$). Moreover, shade only was more effective for *O. leptophyllus* seedling growth than irrigation alone ($P_{I-S+|I+S-} = 0.72$).

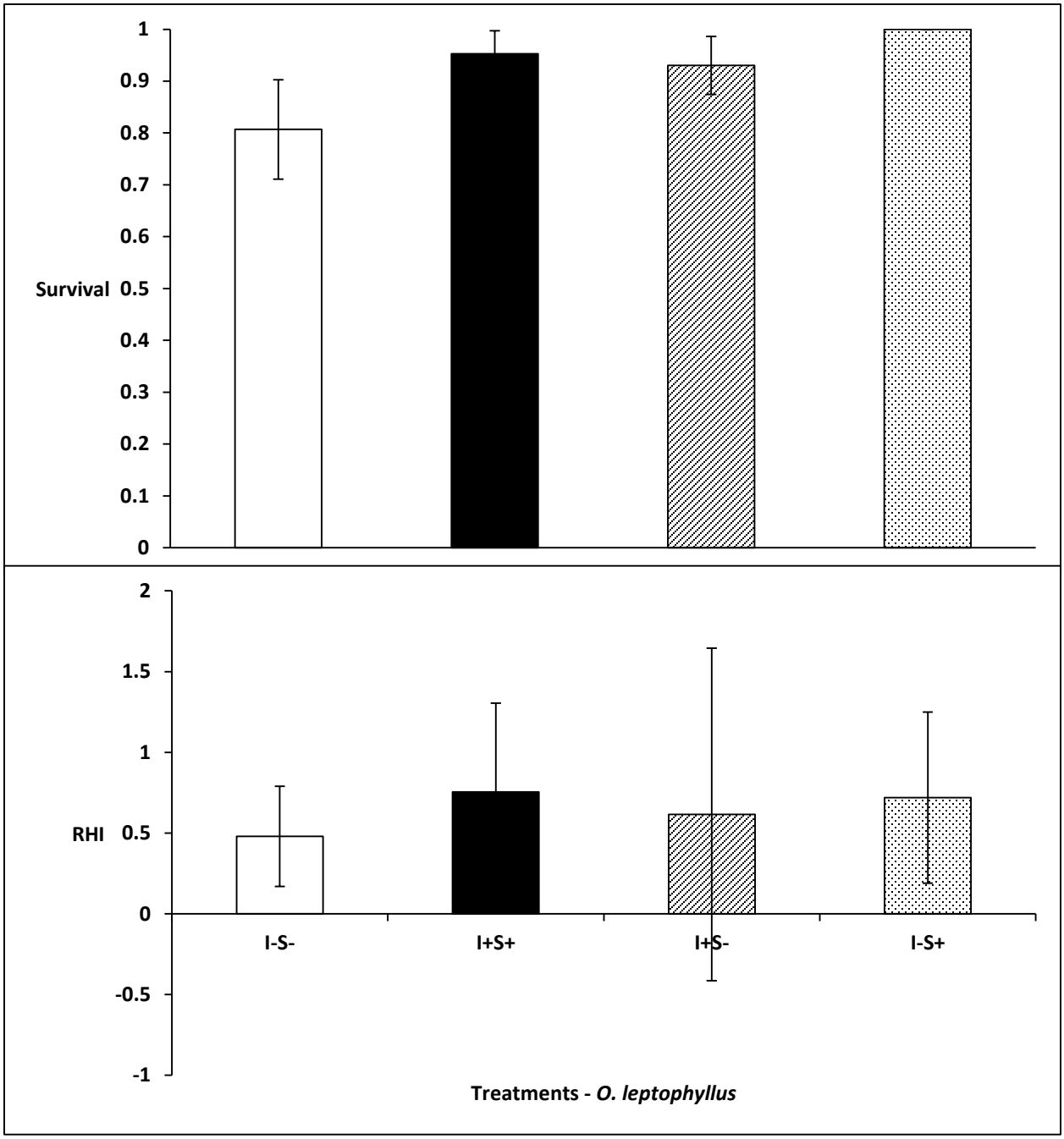


Figure 5-7 Estimated probabilities of survival (A) and Relative Height Increment (B), and respective 95% credible intervals, per treatment, for *Ozothamnus leptophyllus* seedlings. Irrigation Trial.

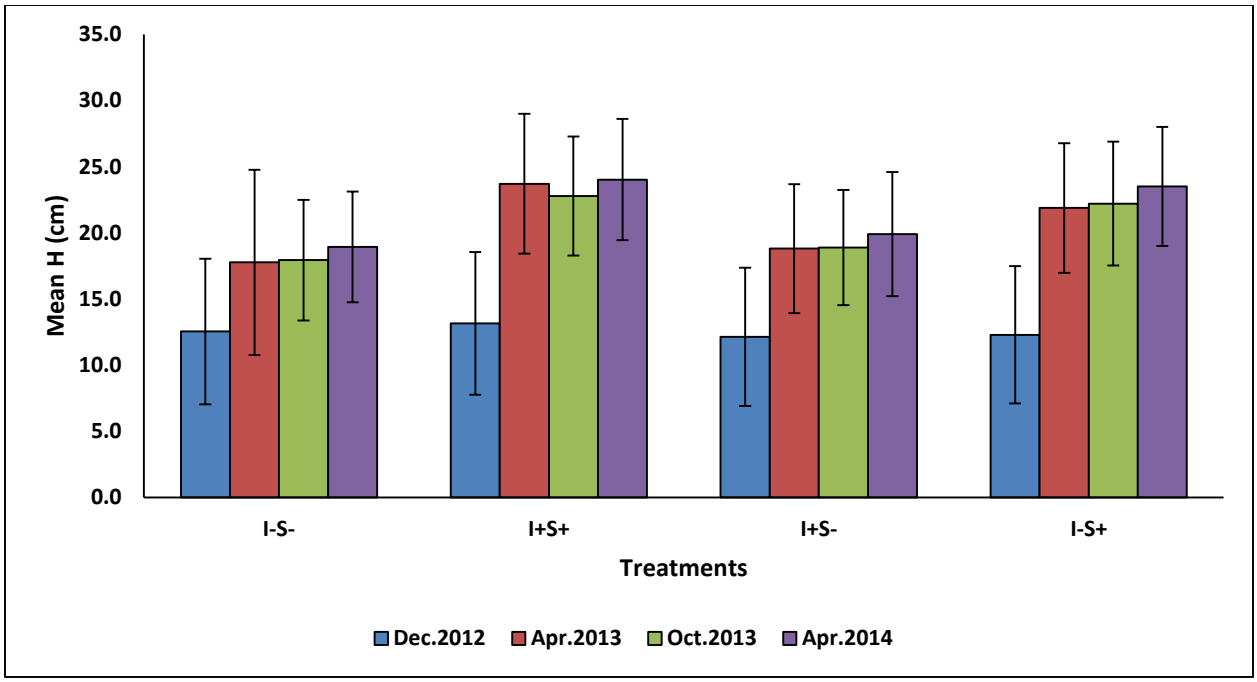


Figure 5-8 Mean heights (cm) of *Ozothamnus leptophyllus* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. Irrigation Trial.

Table 5-6 Comparison of probability of survival among treatments for *Ozothamnus leptophyllus* seedlings. Numbers represent the probability that treatment A in row is superior to the probability of treatment B in column. If $P(trt_A - trt_B) > 0$, then $trt_A > trt_B$. Irrigation Trial.

Treatment	**I-S-**	**I+S+**	**I+S-**	**I-S+**
I-S-	0			
I+S+	0.95	0		
I+S-	0.91	0.34	0	
I-S+	1.00	1.00	1.00	0

Table 5-7 Comparison of RHI among treatments for *Ozothamnus leptophyllus* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column. If $P(trt_A - trt_B) > 0$, then $trt_A > trt_B$. Irrigation Trial.

Treatment	**I-S-**	**I+S+**	**I+S-**	**I-S+**
I-S-	0			
I+S+	0.83	0		
I+S-	0.55	0.23	0	
I-S+	0.77	0.43	0.72	0

5.2.3 *Carbon Isotope analysis - $\delta^{13}C$*

The $\delta^{13}C$ values for *L. scoparium* samples under all four treatments ranged from -27.95 to -29.47‰ (Figure 5-9). Although the most negative levels were recorded for the shaded treatments, the comparisons did not show any statistically strong differences in treatment effect on this parameter, as the Bayesian P values varied between 0.46 and 0.63 (Table 5-8). Average $\delta^{13}C$ values for *O. leptophyllus* seedlings were between -29.48 and -31.64‰ (Figure 5-10), and though averages also tended to be more negative in the shaded treatments, there was not a strong statistical difference among treatments (P = 0.47 ~ 0.67; Table 5-9).

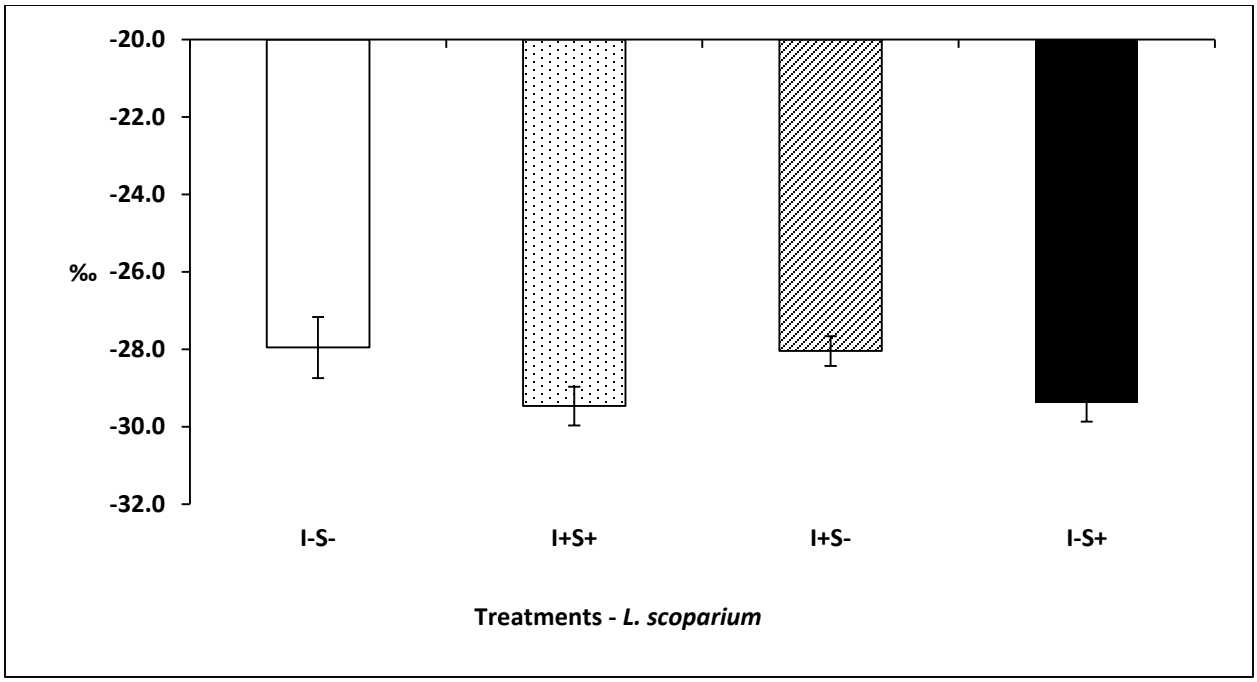


Figure 5-9 Estimated $\delta^{13}C$ values of *Leptospermum scoparium* seedlings and respective 95% credible intervals under each treatment. Irrigation Trial.

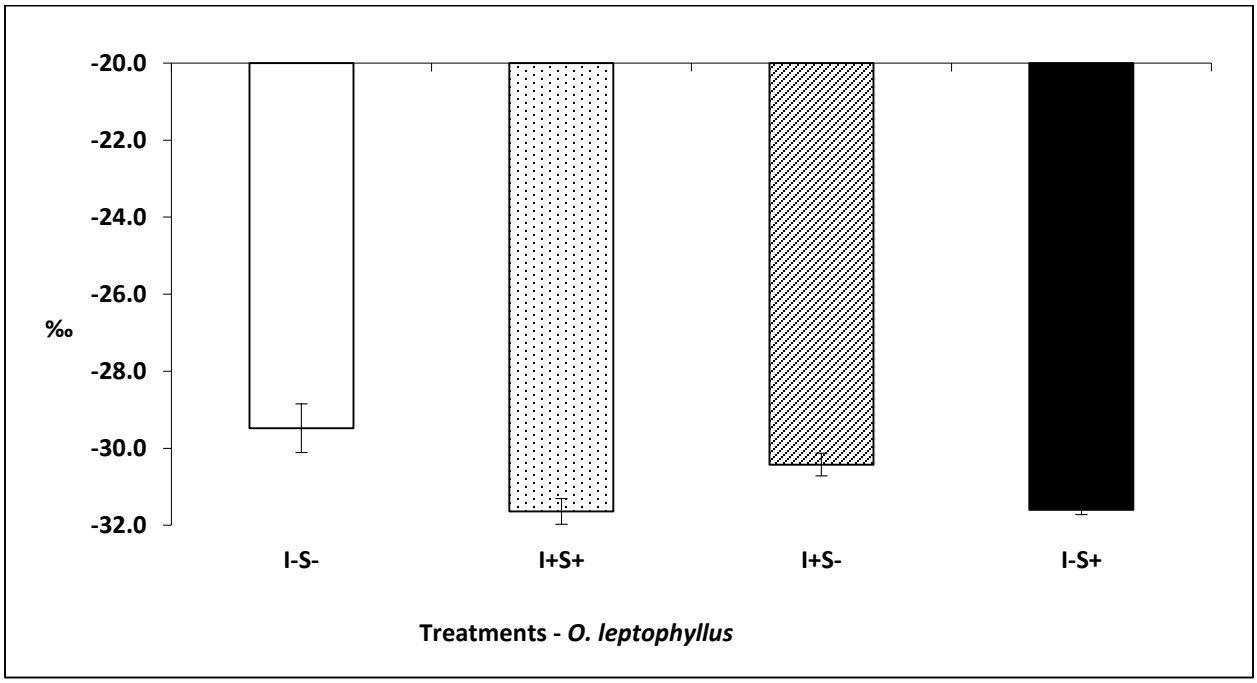


Figure 5-10 Estimated $\delta^{13}C$ values of *Ozothamnus leptophyllus* seedlings and respective 95% credible intervals under each treatment. Irrigation Trial.

Table 5-8 Comparison of $\delta^{13}C$ values among treatments for *L. scoparium* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\delta_A > \delta_B|data)$, where δ refers to estimated $\delta^{13}C$ values. Irrigation Trial.

Treatment	**I-S-**	**I+S+**	**I+S-**	**I-S+**
I-S-	0			
I+S+	0.60	0		
I+S-	0.54	0.46	0	
I-S+	0.63	0.53	0.60	0

Table 5-9 Comparison of estimated $\delta^{13}C$ values among treatments for *O. leptophyllus* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\delta_A > \delta_B|data)$, where δ refers to estimated $\delta^{13}C$ values. Irrigation Trial.

Treatment	**I-S-**	**I+S+**	**I+S-**	**I-S+**
I-S-	0			
I+S+	0.63	0		
I+S-	0.58	0.47	0	
I-S+	0.67	0.53	0.58	0

5.3 Grazing trial

5.3.1 *Soil water content*

Soil water content (Θ) fluctuated across seasons, with the lowest averages in the summer (January-2013 and 2014) and the highest values in early spring (October-2013). Estimated Θ was generally lower than 27% at every period that was monitored except in October-2013, when averages ranged from 38.2% (G+S+) to 44.2% (G-S+). Coincidently, this was the month with the highest monthly precipitation levels of the study period (82.9 mm), and relatively lower air temperatures (14.9°C). In the last monitoring period (March-2014), soil moisture averages were higher than in the beginning of the experiment (Figure 5-11), as were monthly precipitation averages (36.4 mm, Figure 5-1).

The same weather data presented for the Irrigation trial was used for the Grazing trial (see Weather Data – Mackenzie Basin), since both study sites were located in the same farm (Glenmore Station). Therefore, only the results for soil moisture will be presented for the Grazing trial with no reference to the weather data. Refer to 5.2.1 for the results regarding average precipitation and air temperature on the day soil moisture was analyzed (at planting and in January-2014). Estimated Θ at planting was <20% and homogeneously distributed across the study site. In January-2014, averages ranged from 14.76% (G+S-) to 24.31% (G+S+; Figure 5-12). The comparisons among treatments presented in Table 5-10 show the effect of shade only (G+S+) was evident compared to the control ($P_{G+S+|G+S-} = 0.82$) in promoting higher estimated soil moisture levels. Grazing exclusion did not have a substantial effect on this parameter ($P_{G-S-|G+S-}=0.53$), unless combined with shade ($P_{G-S+|G+S-}=0.75$). Soil moisture in the G+S+ was higher than in the G-S+, though statistically the difference between these two treatments may be considered irrelevant ($P_{G+S+|G-S+} = 0.61$).

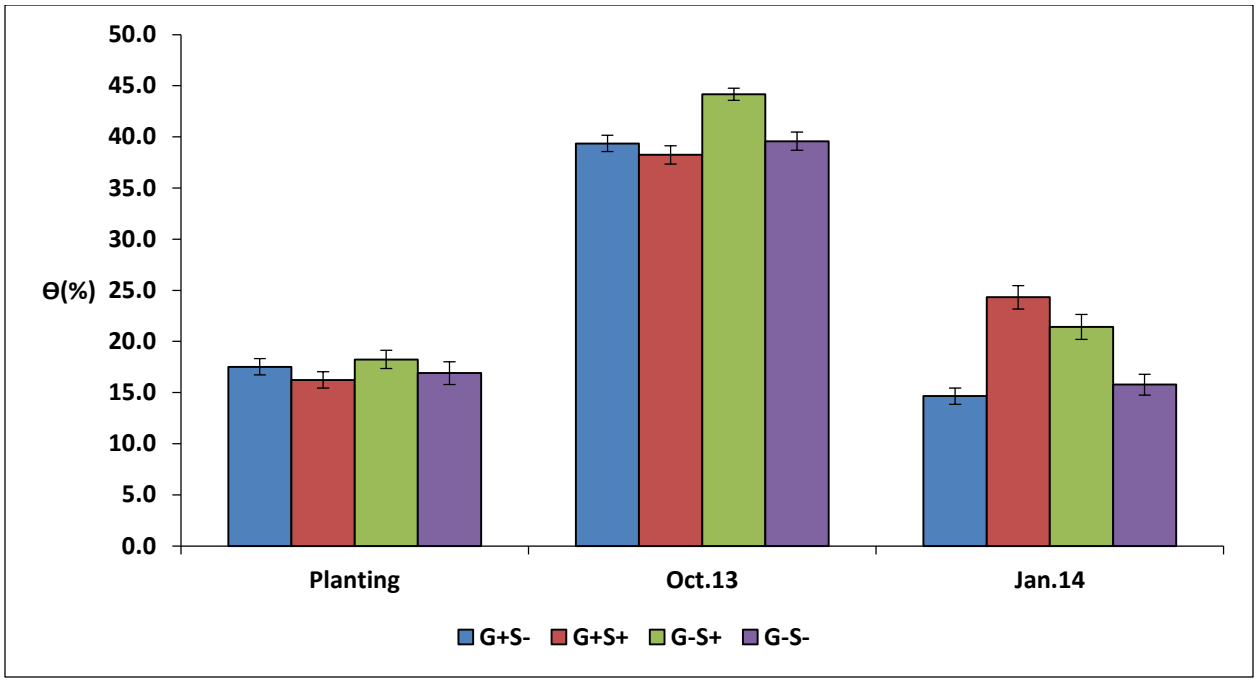


Figure 5-11 Estimated soil water content and respective 95% credible intervals at each monitored period, per treatment. Grazing Trial.

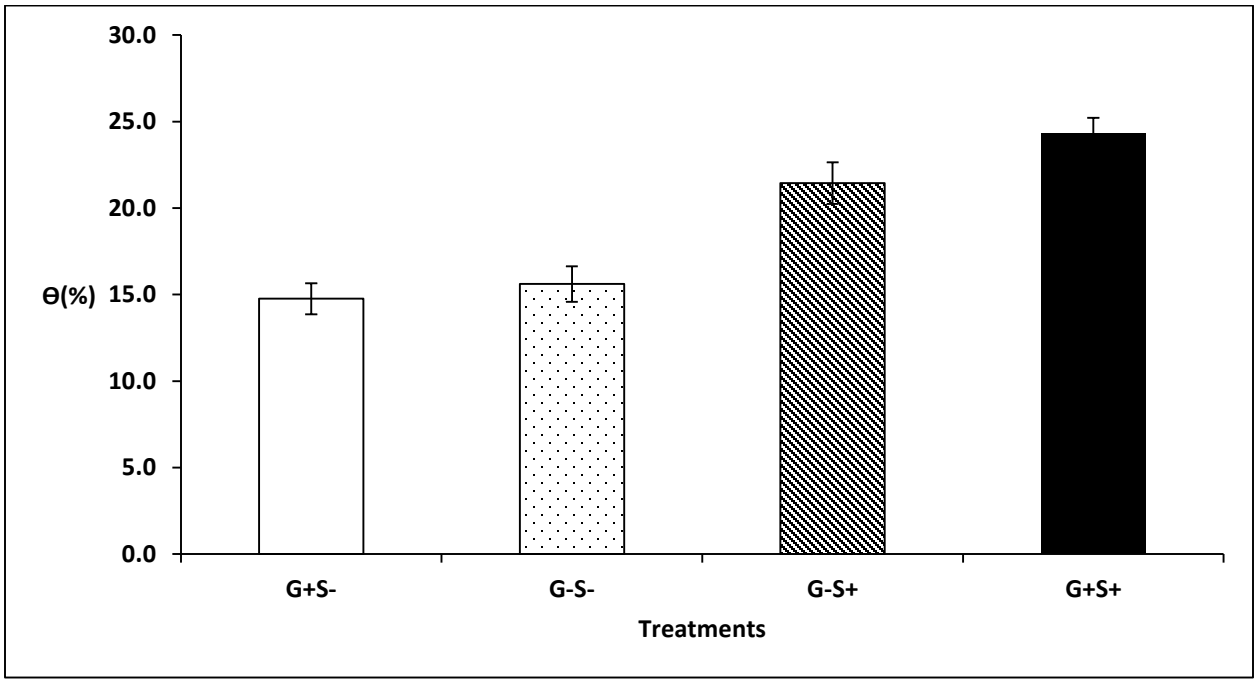


Figure 5-12 Estimated soil water content and respective 95% credible intervals per treatment in January-2014. Grazing Trial.

Table 5-10 Comparison of estimated Θ among treatments in January-2014. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(\Theta_A > \Theta_B|data)$, where Θ refers to estimated soil water content. Grazing Trial.

Treatment	**G+S-**	**G+S+**	**G-S+**	**G-S-**
G+S-	0			
G+S+	0.82	0		
G-S+	0.75	0.39	0	
G-S-	0.53	0.20	0.29	0

5.3.2 *Survival and Growth*

In the Grazing Trial, a total of 91 (47.4%) surviving individuals of *Leptospermum scoparium* and 166 of *Ozothamnus leptophyllus* (86.5%) were present at the end of the experiment (Table 5-11). Seedlings of both species had highest survival rates in the G-S+ treatment and lowest numbers in the control plots (G+S-).

Table 5-11 Number of survivors per plant species, Grazing Trial.

Treatment	***L. scoparium***	***O. leptophyllus***
G+S- (control)	13	37
G+S+	22	41
G-S+	40	44
G-S-	16	44
Total	91	166

Leptospermum scoparium

Leptospermum scoparium seedlings had a higher probability of survival under the G-S+ treatment (0.87). As for the remaining treatments, probabilities were < 0.50 (Figure 5-13A). The statistical analyses in Table 5-12 show a strong treatment effect on seedling survival compared to the control ($P \geq 0.75$). Shade alone had stronger effects on seedling survival compared to control ($P_{G+S+|G+S-} = 0.92$). Grazing exclusion was more effective than control when combined with shade ($P = 1.00$), although probabilities in the grazing-only plots were also higher than in the control ($P = 0.75$). Fencing alone also promoted higher seedling probability of survival compared to G+S+ ($P_{G-S+|G+S+} = 0.99$). However, G-S- was statistically less effective than G-S+ ($P_{G-S-|G-S+} = 0.00$) and also less effective than G+S+ ($P_{G-S-|G+S+} = 0.23$).

L. scoparium seedlings at the start of the experiment had mean heights ranging from 36.8 cm to 39.5 cm, which continuously decreased until the end of the experiment (Figure 5-14). In April-2013, seedling mean heights were between 23.4 cm (G+S-) and 30.4 cm (G-S+). From winter to early spring, in October-2013, seedlings dieback resulted in mean heights ranging from 8.5 cm (G+S-) to 27.4 cm (G-S+). By the end of the trial, mean heights of *L. scoparium* seedlings in April-2014 ranged from 8.5 cm (G+S- or control) to 27.4 cm (G-S+). Consequently, *L. scoparium seedlings* had negative RHI values under all treatments in the Grazing trial (Figure 5-13B). Seedling dieback was most intense in the control plots (RHI = -1.40) and least pronounced in the G-S+ (RHI = -0.37). Simulations in Table 5-13 indicate a stronger effect of shade than grazing exclusion on *L. scoparium* seedling RHI ($P_{G+S+|G-S-} = 0.89$). The stronger effect of shade over fencing could also be detected when comparing both no-grazing treatments ($P_{G-S+|G-S-} = 0.99$). Nevertheless, some of the *L. scoparium* seedlings planted in the grazing treatments (G+S+ and G+S-) still suffered predation (Figure 5-17).

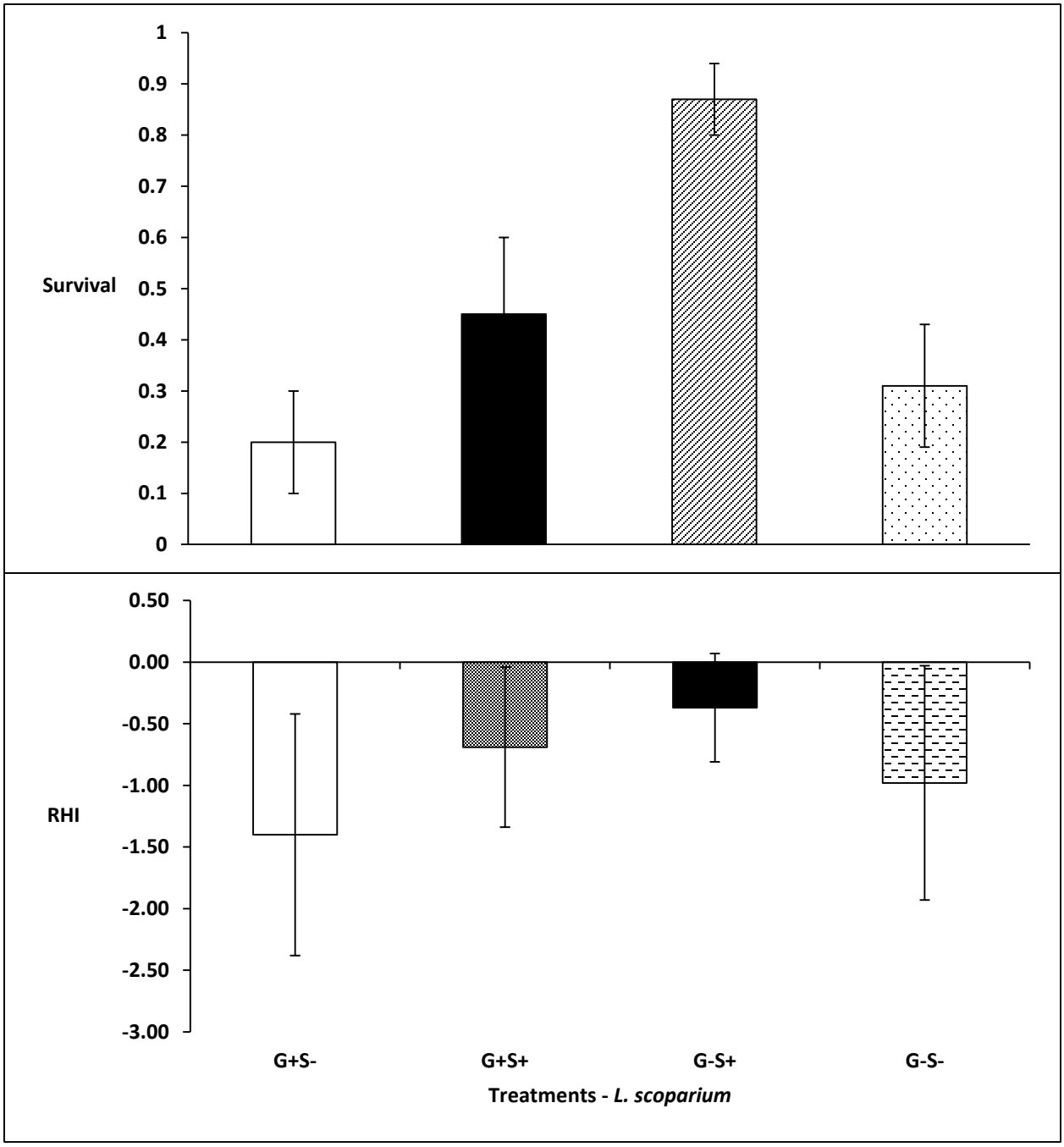


Figure 5-13 Estimated probabilities of survival (A) and Relative Height Increment (B), and respective 95% credible intervals, per treatment, for *Leptospermum scoparium* seedlings. Grazing Trial.

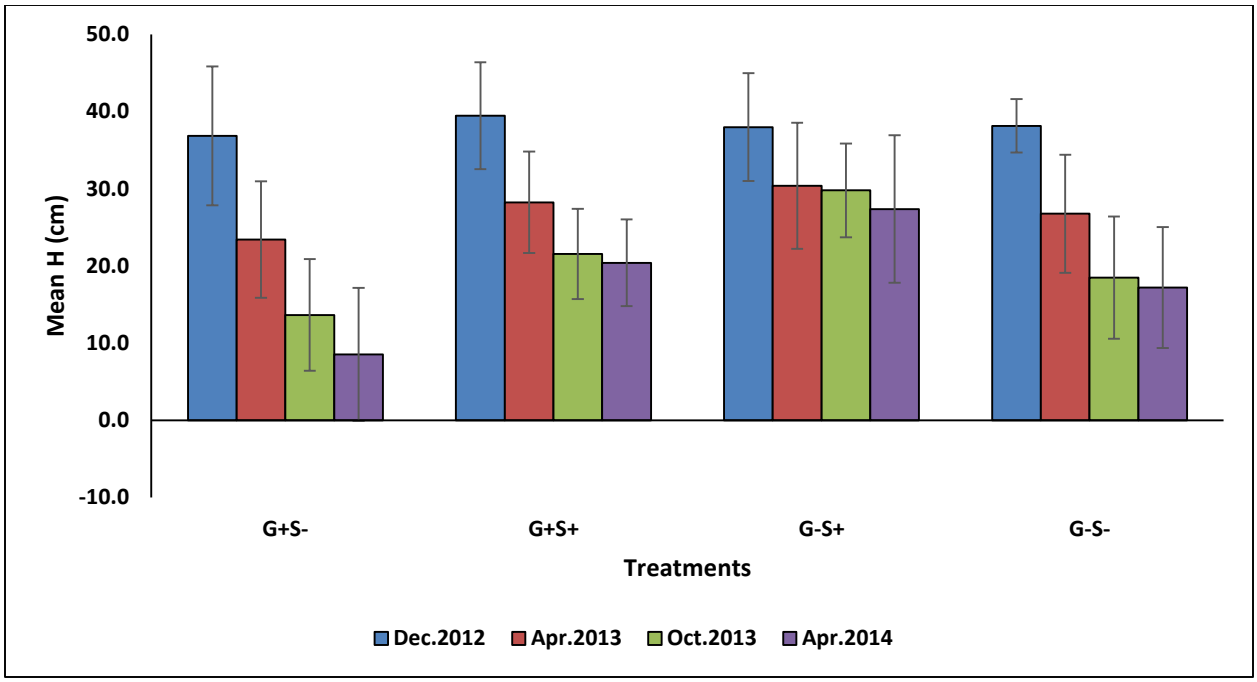


Figure 5-14 Mean heights (cm) of *Leptospermum scoparium* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. Grazing Trial.

Table 5-12 Comparison of probability of survival among treatments for *Leptospermum scoparium* seedlings. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., P($estS_A > estS_B$|data), where estS refers to estimated probability of survival. Grazing Trial.

Treatment	**G+S-**	**G+S+**	**G-S+**	**G-S-**
G+S-	0			
G+S+	0.92	0		
G-S+	1.00	0.99	0	
G-S-	0.75	0.23	0.00	0

Table 5-13 Comparison of estimated RHI of *Leptospermum scoparium* seedlings among treatments. Numbers represent the proportion of times for which treatment A in row is superior to treatment B in column, i.e., $P(RHI_A > RHI_B|data)$. Grazing Trial.

Treatment	G+S-	G+S+	G-S+	G-S-
G+S-	0			
G+S+	0.99	0		
G-S+	0.99	0.92	0	
G-S-	0.89	0.11	0.01	0

Ozothamnus leptophyllus

Ozothamnus leptophyllus seedlings had probability of survival ≥ 0.80 under all treatments in the Grazing trial, including the control (Figure 5-15A). Seedlings responded more strongly to both no-grazing treatments (0.93), as well as to shade only (G+S+ = 0.86). Simulations show a strong treatment effect on *O. leptophyllus* seedling survival compared to the control (Table 5-14). Shade had more beneficial effects on the probability of survival of *O. leptophyllus* seedlings than the control ($P_{G+S+|G+S-} = 0.79$), although the effects of grazing exclusion were markedly higher even in the absence of shade ($P_{G-S-|G+S-} = 0.96$), as were the effects of both treatments combined ($P_{G-S+|G+S-} = 0.94$). The comparisons also show that both no-grazing treatments had statistically similar effects on the probability of survival of *O. leptophyllus* seedlings ($P_{G-S-|G-S+} = 0.51$).

Figure 5-16 shows that the mean height of *O. leptophyllus* seedlings at planting ranged from 13.8 cm to 15.5 cm. Mean heights of seedlings increased during the first summer and in April-2013, and averages ranged from 18.3 cm (G+S-) to 22.4 cm (G-S+). From April to October-2013, mean heights of seedlings decreased the G+S-, G+S+, and G-S- treatments, and had a small increase in the G-S+ plots. *O. leptophyllus* seedlings continued growing in the next measurement season under all treatments and, by April-2014, mean heights ranged from 17.0 cm (G+S-) to 25.1 cm (G-S+). Hence, *O. leptophyllus* seedlings had a positive RHI in the Grazing trial under all treatments (Figure 5-15B). Simulations in Table 5-15 show that grazing exclusion alone had a strong and positive effect on seedling growth compared to the control ($P_{G-S-|G+S-} = 0.77$), and the

effect was more evident when shade was included ($P_{G\text{-}S+|G+S-} = 0.98$). However, shade alone had no distinguishing effect on RHI compared to the control ($P_{G+S+|G+S-} = 0.53$). Herbivore feces, probably of hares or rabbits, and damaged seedlings in the grazing plots were photographically registered (Figure 5-17, Figure 5-18 and Figure 5-19).

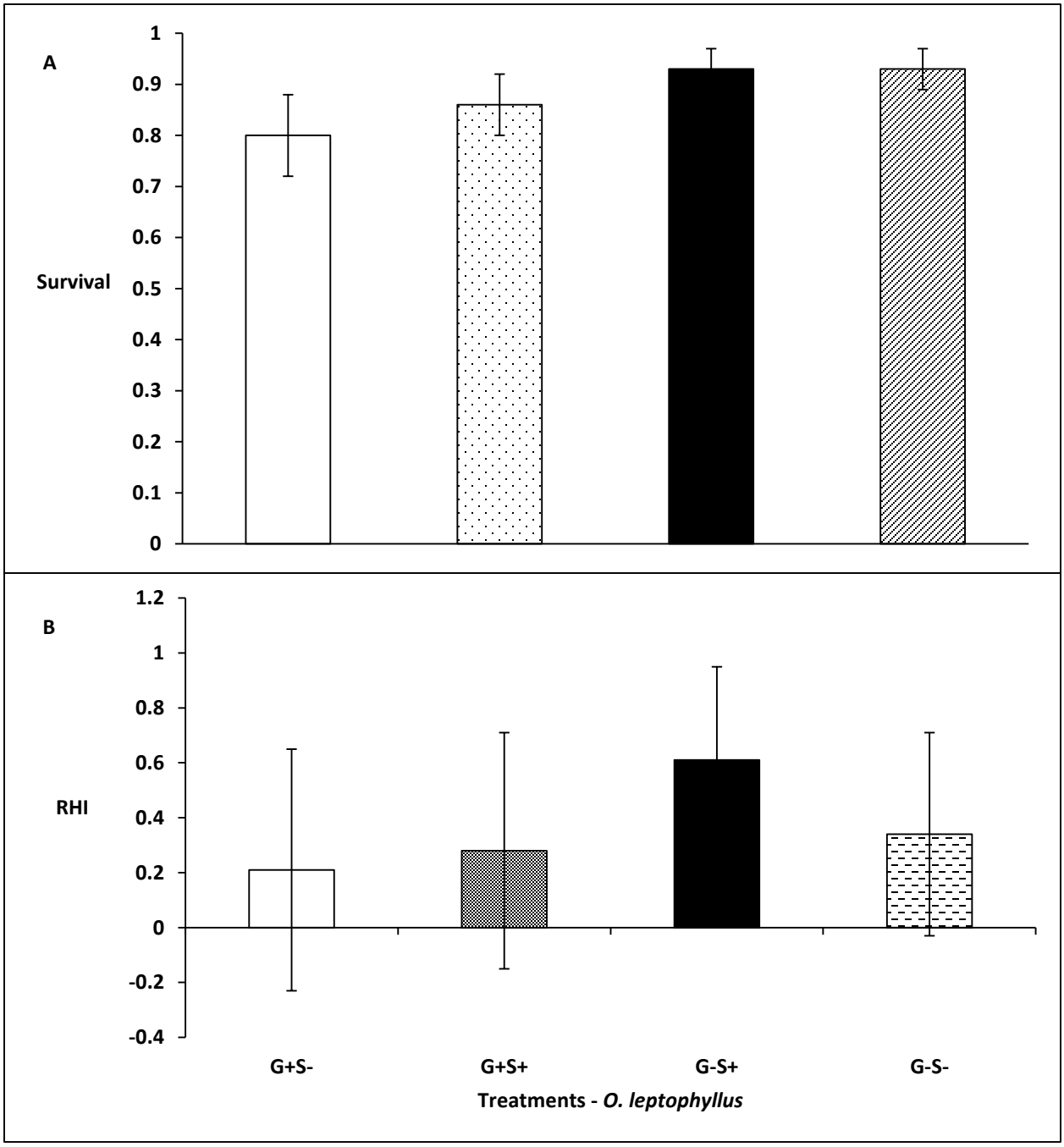


Figure 5-15 Estimated probabilities of survival (A) and Relative Height Increment (B), and respective 95% credible intervals, per treatment, for *Ozothamnus leptophyllus* seedlings. Grazing Trial.

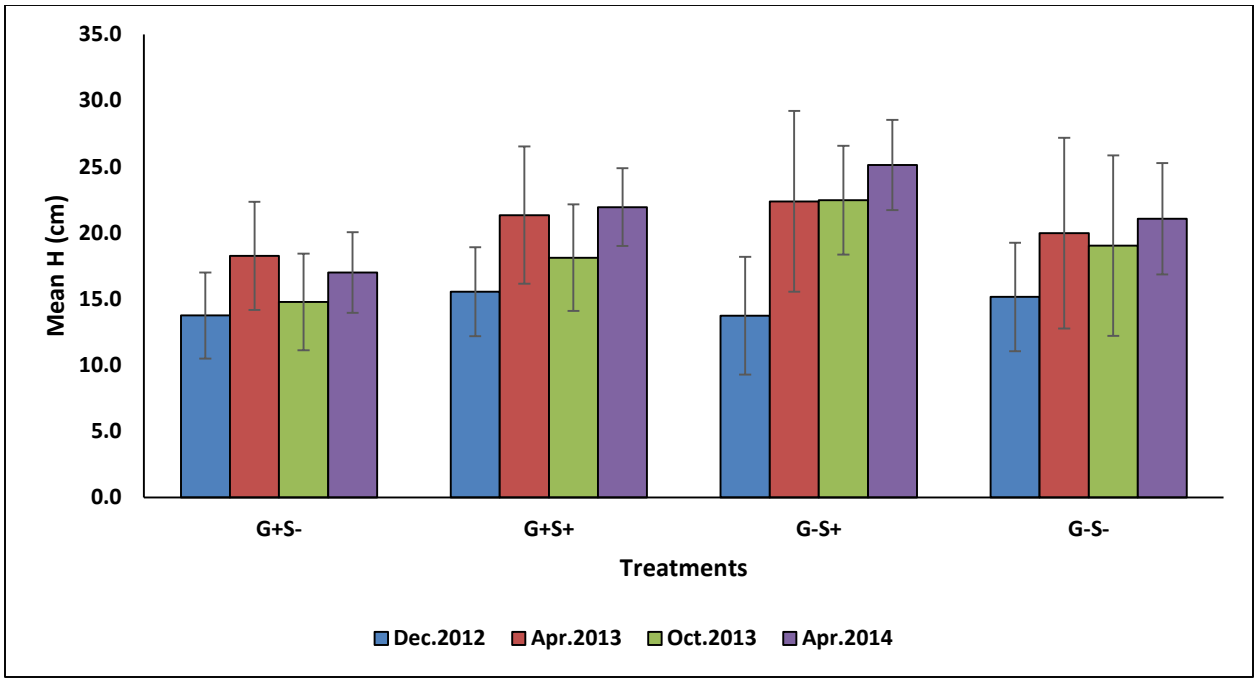


Figure 5-16 Mean heights (cm) of *Ozothamnus leptophyllus* seedlings, per treatment, and respective 95% credible intervals at different measurement periods. Grazing Trial.

Table 5-14 Comparison of estimated probability of survival among treatments for *Ozothamnus leptophyllus* seedlings. Numbers represent the probability that treatment A in column is superior to the probability of treatment B in row. If $P(trt_A - trt_B) > 0$, then $trt_A > trt_B$. Grazing Trial.

Treatment	**G+S-**	**G+S+**	**G-S+**	**G-S-**
G+S-	0			
G+S+	0.79	0		
G-S+	0.94	0.82	0	
G-S-	0.96	0.85	0.51	0

Table 5-15 Comparison of estimated RHI among treatments for *Ozothamnus leptophyllus* seedlings. Numbers represent the probability that treatment A in column is superior to the probability of treatment B in row. If $P(trt_A - trt_B) > 0$, then $trt_A > trt_B$. Grazing Trial.

Treatment	**G+S-**	**G+S+**	**G-S+**	**G-S-**
G+S-	0			
G+S+	0.53	0		
G-S+	0.98	0.96	0	
G-S-	0.70	0.67	0.07	0

Figure 5-17 *Leptospermum scoparium* seedling in grazing (unfenced) plot that lost its main stem likely due to hare browse. Grazing Trial.

Figure 5-18 *Ozothamnus leptophyllus* seedling in a grazing (unfenced) plot that lost part of its main stem likely due to browsing. Grazing Trial.

Figure 5-19 Rabbit or hare feces found in a grazing (unfenced) plot and evidence of browsing on *Ozothamnus leptophyllus* seedlings (red circles mark some plant parts found on the ground). Grazing Trial.

5.3.3 *Carbon Isotope analysis - $\delta^{13}C$*

Estimated $\delta^{13}C$ values of *L. scoparium* seedlings ranged from -26.55 to -28.80‰ (Figure 5-20). Estimates were relatively more negative in the shaded treatments (G+S+ and G-S+), however, the averages were not statistically different among all treatments (Table 5-16). Estimated $\delta^{13}C$ values of *Ozothamnus leptophyllus* seedlings ranged from -29.15 to -31.38‰ (Figure 5-21). The lowest (or more negative) values were obtained for seedlings in the shaded treatments, although differences among treatments were not statistically substantial (Table 5-17).

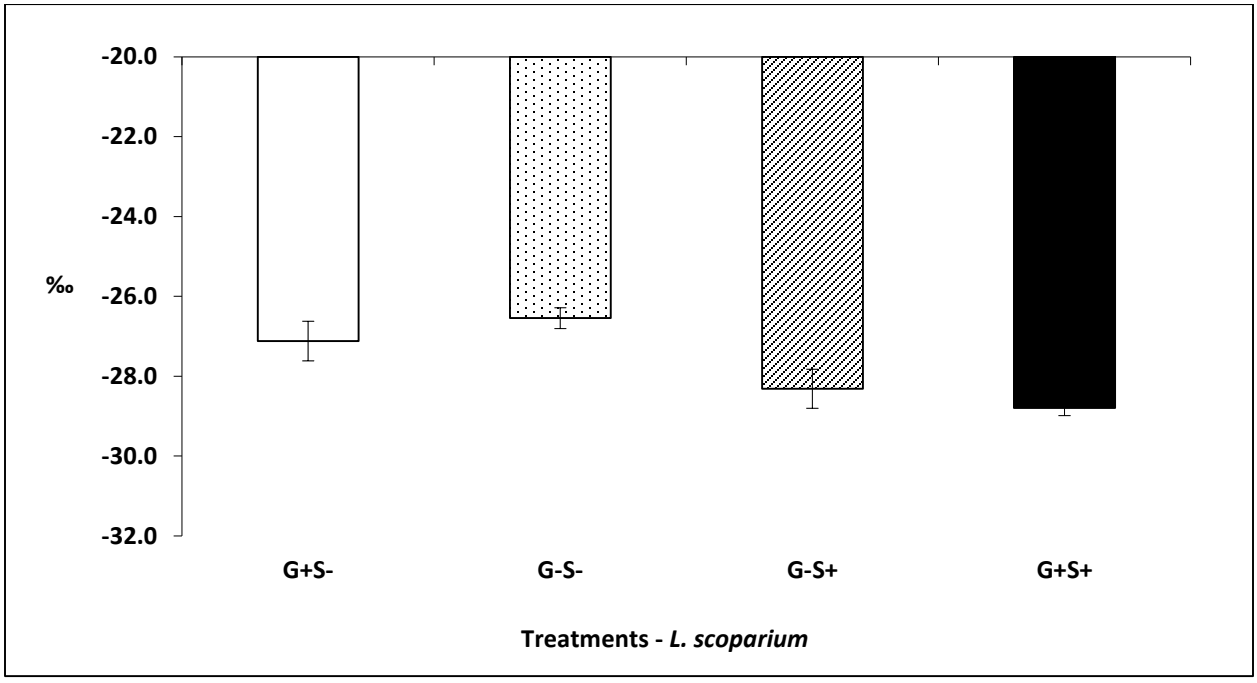


Figure 5-20 Estimated $\delta^{13}C$ values and respective 95% credible intervals of *Leptospermum scoparium* seedlings per treatment type. Grazing Trial.

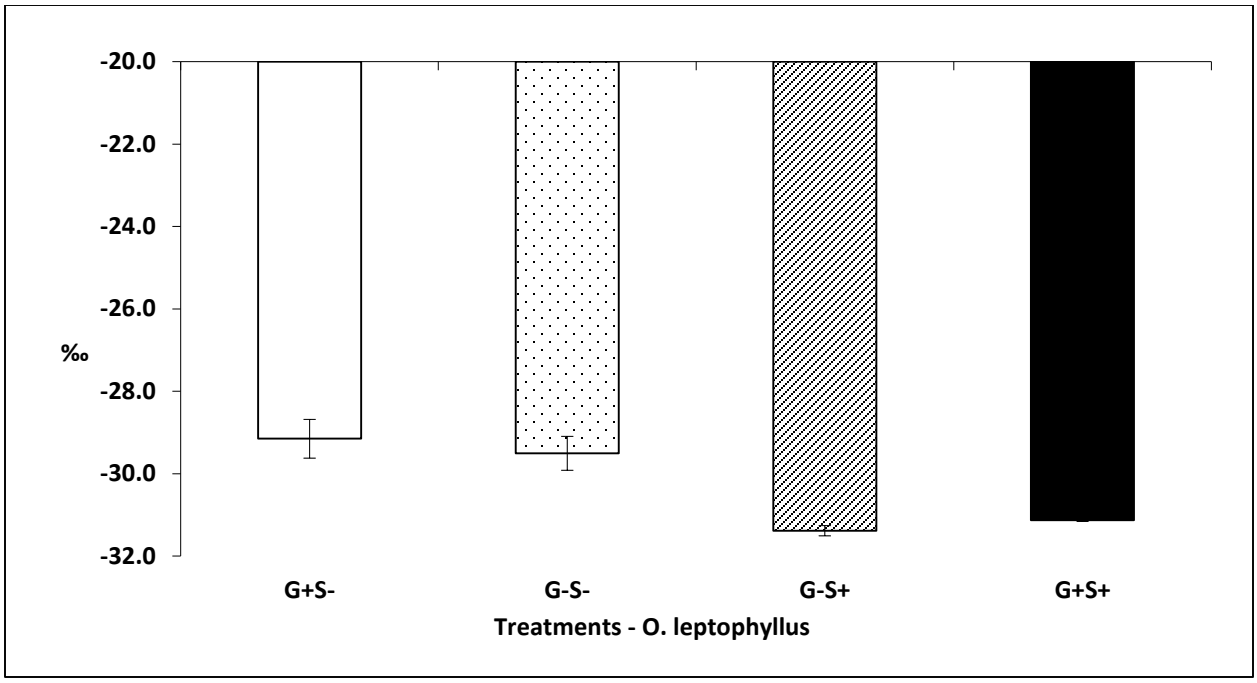


Figure 5-21 Estimated $\delta^{13}C$ values and respective 95% credible intervals for *Ozothamnus leptophyllus* seedlings, per treatment. Grazing Trial.

Table 5-16 Comparison of δ13C values of *Leptospermum scoparium* seedlings among treatments. Numbers represent the posterior probability that treatment in column A is superior to treatment in row B, i.e., $P(\delta_A > \delta_B|data)$, where δ refers to estimated $\delta^{13}C$ values. Grazing Trial.

Treatment	**G+S-**	**G+S+**	**G-S+**	**G-S-**
G+S-	0			
G+S+	0.60	0		
G-S+	0.50	0.38	0	
G-S-	0.61	0.49	0.62	0

Table 5-17 Comparison of estimated $\delta^{13}C$ values of *Ozothamnus leptophyllus* seedlings among treatments. Numbers represent the posterior probability that treatment in column A is superior to treatment in row B, i.e., $P(\delta_A > \delta_B|data)$, where δ refers to estimated $\delta^{13}C$ values. Grazing Trial.

Treatment	**G+S-**	**G+S+**	**G-S+**	**G-S-**
G+S-	0			
G+S+	0.66	0		
G-S+	0.56	0.38	0	
G-S-	0.63	0.46	0.58	0

5.4 Discussion

5.4.1 *Effects of Shade*

The results show that, although there were some varying responses to treatment type at the species level, *Leptospermum scoparium* and *Ozothamnus leptophyllus* seedlings planted in the Degraded Short Tussock sites, in general, had highest probability of survival and relative height increments in the shaded treatments. Supplemental water (Irrigation trial only) and fencing (Grazing trial only) also promoted some positive effects on the seedlings' establishment and growth. However, more substantial results were obtained when either irrigation or fencing was combined with shade. Shade was, therefore, the only treatment that consistently promoted more positive responses of the seedlings throughout the experimental period in both the Irrigation and Grazing trials. The seedlings' responses to shade can be related to the relatively higher soil moisture levels in these treatments. The increased soil moisture can in turn be related to improved local microclimate in shaded conditions as a consequence of reduced air and soil temperatures (Callaway, 1995; Baumeister & Callaway, 2006). However, soil water averages remained ≤ 30% under most treatments (except irrigated plots) and during most of the experimental period. These averages can be considered low according to Fredlund et al. (2002). In this case, the study sites' soil type may offer an explanation to why soil water levels were generally under 30% even in the shaded treatments. Textural information from the upper 30 cm of the soil profile has been used to assign water-holding attributes to the entire soil profile (Webb et al., 1993a) or the root zone (Groenendijk, 1989), though a realistic value of available soil water can only be interactively estimated as a combined function of climate, soil, and vegetation(Webb et al., 1993a). According to the model proposed by Fredlund et al. (2002), soil water potential for silty clay loam soils, such as those found in the study sites (see Appendix: Soil Physical Analyses – Soil Classification), increases exponentially as gravimetric water content reaches levels lower than 30%, and water availability to plants decreases. Hence, it is possible that the study sites' soils have a naturally low water-holding capacity due to their textural characteristics. The reduced soil water content is likely aggravated by soil compaction and climate (Saxton & Rawls, 2006) which, consequently, impact soil water availability to plants (Yates et al., 2000; Nawaz et al., 2013).

The typically elevated air temperatures and high wind speeds in the summer in the Mackenzie Basin, combined with the exposure of the soil surface to direct solar radiation, probably increased the daily evapotranspiration rates during this period of the year, and intensified water deficit to the restoration seedlings due to reduced soil moisture in unshaded and unirrigated conditions (Lockart et al., 2013). Seedling responses to shade in the Irrigation and Grazing trials support the hypothesis that seedling establishment and growth would be higher if sheltered from the local weather elements. Either artificial or natural shelter from direct solar radiation and exposure to high winds have been reported to reduce surface soil temperature extremes by up to 10-12°C (Wilson, 1996), to increase soil moisture and to be the main facilitative mechanism of woody seedling species establishment (Maestre et al., 2003; Benayas et al., 2005). Soil moisture directly influences the air temperature immediately above the soil surface, and controls evapotranspiration rates (Nicholls, 2004; Cavanaugh et al., 2011). The higher proportion of seedling mortality in the unshaded treatments can be linked to physiological failure associated with water stress-related desiccation, a common pattern observed in restoration efforts of abandoned farmlands and other secondary habitats (Hammond, 1995).

In contrast to this, the estimated $\delta^{13}C$ values obtained from leaf samples of the surviving seedlings were within the observed average for healthy, unstressed and photosynthetically efficient C3 plants (Griffiths, 1991). Therefore, it could be argued that *L. scoparium* and *O. leptophyllus* seedlings were not suffering from water stress in any of the treatments at the time the leaf samples were taken if $\delta^{13}C$ were the only parameter used to assess this. Apart from a small tendency to a more negative $\delta^{13}C$ level in the shaded and irrigated plots, the differences among treatments were not statistically significant and could not lead to any significant conclusions regarding water stress in seedlings, treatment type and soil moisture. Other studies have also found no definitive relationship between $\delta^{13}C$ values and soil moisture levels. For example, eucalyptus trees in Northern Australia showed no differences in $\delta^{13}C$ measurements of several trees across a gradient of soil water content, even towards the end of the dry season, when low soil moisture is most pronounced (Cernusak et al., 2013). This can be attributed to a conservative water use strategy commonly found in drought-tolerant dryland plant species (Moreno-Gutiérrez et al., 2012) and, therefore, responsible for the statistically similar carbon isotopic responses of the native seedlings to the different treatments. Several environmental

conditions can act as stressors to plants and influence their photosynthetic rates or stomatal conductance, thus affecting cellular carbon concentration and $\delta^{13}C$ ratio in plant biomass (Gebrekirstos et al., 2011). However, drought tolerant plants that present a conservative water use strategy are capable of maintaining low (more negative) and relatively unaltered $\delta^{13}C$ values when soil moisture levels change (Moreno-Gutiérrez et al., 2012). Another characteristic of plants that present a conservative water use strategy is the $\delta^{13}C$ close to the lowest limit for C3 plants (-32‰) (Ehleringer et al., 1993), an indication of high water-use efficiency in these plants (Gebrekirstos et al., 2011). High water-use efficiency enables plants to continue growing, however slowly, even when resources such as soil water are limiting (Farquhar et al., 1989a; Moreno-Gutiérrez et al., 2012). The $\delta^{13}C$ and growth results obtained in the Degraded Short Tussock may be a considerable support for the hypothesis that *L. scoparium* and *O. leptophyllus* seedlings present a conservative water use strategy. However, other measurements such as stomatal conductance and water potentials would be necessary to verify this theory.

Based on the survival and growth data, it may be assumed that the mean $\delta^{13}C$ values of the native seedlings in the Degraded Short Tussock trials could have simply reflected another physiological strategy of young plants in which they down-regulate their photosynthetic demand for CO_2 to compensate stomatal closure caused by water deficit (Ort et al., 1994; Chaves et al., 2002). Water stress can trigger this protective mechanism in plants when they are under high light and temperature conditions (Chaves et al., 2002; Cernusak et al., 2011). The estimated $\delta^{13}C$ values of the *L. scoparium* and *O. leptophyllus* seedlings were similar to the averages observed by Chaves et al. (2002) in water-stressed white-lupin plants, which were more negative than in well-watered plants, reflecting a more elevated ^{13}C:^{12}C ratio. Havaux (1992) observed a similar pattern in Solanaceae plants that, in dehydrating conditions at high temperatures (38-40°C), presented much less inhibited photosynthesis than well-watered plants in the same environmental condition.

The estimated $\delta^{13}C$ values of *L. scoparium* and *O. leptophyllus* seedlings may be connected with the morphological characteristics of early successional species (Mason et al., 2011), which enable plants to be more tolerant to harsher environmental conditions (Stephens et al., 2005), such as poor soils (Schönberger, 2002), competition from grasses (*O. leptophyllus*, Wardle 2002,

both extremes of moisture regime (*L. scoparium* Burrell 1965), and tolerant to a wide range of soil physical and chemical conditions (Ronghua et al., 1984). Their morphological characteristics, such as slender branchlets, small and narrow leaves (Wardle et al., 1973; Johnson, 1980; Schönberger, 2002) are typical of evergreen plants from arid and semi-arid ecosystems. These features promote protective measures for plants to cope with water scarcity, extreme temperatures, and high irradiance (Givnish, 1999). Therefore, both mechanical and physiological protective mechanisms were likely responsible for the apparent unstressed state of the restoration seedlings in the Degraded Short Tussock experiments (Chaves et al., 2002; Cornic & Fresneau, 2002; Lawlor, 2002).

5.4.2 Effects of Irrigation

Annual precipitation levels in the Tekapo region are normally below 800 mm (http://cliflo.niwa.co.nz/) and the accumulated precipitation for the period in which the experiment was carried out was within the annual average levels recorded for the last 40 years for the region (2006 Glenmore Station Environmental Report). As shown in the results, annual rainfall was not evenly distributed through the study period, tending to concentrate in the cooler seasons and to drastically reduce in the summer. Areas where there is a pronounced drought period with elevated temperatures can be challenging for restoration activities, where growth and establishment of natural vegetation is more limited by available soil water than by other resources (Caldwell et al., 2009). Thus, even low amounts of supplemental water, applied at the right time, can improve the germination and establishment of native seeds and seedlings (Roundy et al., 2001). The results showed that the native seedlings used in this research did respond more positively to supplemental water in the Irrigation trial compared to those planted in the control plots. Anderson and Ostler (2002) found that the addition of 112 mm of irrigation water to a Mojave Desert site with natural annual precipitation of 130 mm markedly enhanced the germination of native shrubs over control plots without irrigation. Native tall shrubs' relative heights also increased more rapidly under continuous irrigation than under periodic-irrigation over 12 years in a semi-arid Mediterranean site (Gómez-Aparicio et al., 2004).

Seedling dieback and slow growth, however, were not prevented by the supplemental water in the absence of shade, especially for *L. scoparium* seedlings. This was likely due to a growth

depression at high-light conditions that may have taken place even in the seedlings that were continuously irrigated, but exposed to direct sunlight, because of physiological responses triggered by increased irradiance and temperatures (Poorter, 1999). Such conditions force the plant to reallocate biomass to roots instead of shoot to reduce the detrimental effects of aboveground environmental stress (Chaves et al. 2002). Root biomass was not measured in this experiment, so the shoot:root ratio could not be empirically verified in order to confirm this hypothesis; however, it is possible that the surviving seedlings in both the Irrigation and Grazing trials may have been able to survive through this mechanism. Adaptations to high light environments has been noted for New Zealand plant species (Bee et al., 2007). Some plants may reduce stem length and canopy leaves, or produce smaller leaves and stem diameter in order to prevent photoinhibition (Christian et al., 2006). Plants with such characteristics tend to partition a greater proportion of new biomass to roots instead of leaves during the first years of establishment (Wright & Westoby, 2000; Westoby et al., 2002) likely to reduce transpirational losses and increase chances of survival in water-stress and high light conditions (Martin-Vertedor & Dodd, 2011).

Exotic weed and herb densities in the irrigated plots also seemed to have increased during the experiment (personal observation). This type of response from invasive plant species has also been noted in the literature (Sorte et al., 2013), as both exotic and native plants do tend to respond positively as resources increase (Grotkopp et al., 2010). Therefore, exotic weeds present on the Irrigation site were likely to have taken advantage of the supplemental water as well. The additional water supply in the Irrigation trial did not have quite a statistically strong impact on the growth of *L. scoparium* and *O. leptophyllus* seedlings, unless it was combined with shade. The slower response of the native seedlings to increased water supply could eventually lead to an inversed result for restoration in the long-run if irrigation continued (Boswell & Espie, 1998). As suggested by Byers and Noonburg (2003), invasion success of exotic species has a positive correlation with increased resource, but only if native species richness remains constant or has a slight increase. Banerjee et al. (2006) observed that irrigation increased general plant cover on plots in an abandoned farmland at a desert site in Phoenix, Arizona – USA, but exotic weeds remained dominant in both irrigated and unirrigated plots, and probably continued affecting the establishment of native plants in these situations.

5.4.3 *Effects of Grazing*

The impacts of herbivory on the native seedlings were evident in the Grazing trial, where *O. leptophyllus* seedlings and, to a certain degree, *L. scoparium* seedlings, were damaged by grazing. Although regarded in the literature as an unpalatable species (Craine et al., 2006), the growth of *O. leptophyllus* seedlings was significantly affected by the absence of the fence around the respective plots. This indicates that *O. leptophyllus* can be a target for local herbivores – most likely rabbits and hares, and possibly sheep too. The RHI and survival data showed that predation affected mostly this species' overall shoot height increment without necessarily killing the plant. *O. leptophyllus* seemed quite resilient to the site conditions and results suggested that even those plants that were damaged by herbivores and desiccation were capable of resuming growth afterwards. It has been noted in the literature that *O. leptophyllus* has the ability to produce fresh shoots from the base of the stem if the shrub has been damaged (Roy & New Zealand Plant Protection, 2004).

As for *L. scoparium* seedlings, photographic evidence showed that, while some seedlings suffered predation attempts (what looked like "disposed" plant parts on the ground), this species was more vulnerable to the effects of direct sunlight than herbivory. Probability of survival and growth were statistically greater in the G+S+ plots than in the G-S-. Therefore, the data indicate that most *L. scoparium* seedlings probably died from shoot desiccation caused by exposure to high irradiation and temperatures, and consequently water stress, instead of from predation. The predation attempt and eventual damage to *L. scoparium* seedlings in the Grazing trial could have been a collateral effect of the predation on *O. leptophyllus* seedlings or on the existing short-tussock and *Hieracium* plants. The so-called plant-damage probability (Etzenhouser et al., 1998) is applied to the associational defense of palatable plants in a matrix of unpalatable ones in order to avoid being browsed. However, it is possible that the opposite effect could have taken place in the Grazing trial concerning *L. scoparium* seedlings, where one unpalatable plant was surrounded by other more appealing food source. The discarded *L. scoparium* seedling parts evidenced in the photos may have been caused by the typical behavior of herbivores that, after finding a good food source, they assess the immediate surroundings for more potential food availability, thus causing damages to other less attractive plant species in the process (Rees et al., 2001; Baraza et al., 2006).

Fencing, however, can have the undesirable effect on increasing exotic weed density (Scott et al., 2001; Rose et al., 2004), although in New Zealand, fencing is almost always essential for restoration of native woody seedlings, since native plants did not evolve in the presence of mammalian herbivores (Walker et al., 2009b). It was observed that the cover of weed and herb species became denser within the fenced plots in the Grazing trial, similarly to what Scott et al. (2001) observed on an overgrazed tussock-grassland in the upper Waitaki Valley, South Island, New Zealand. The relative height increment of *L. scoparium* and *O. leptophyllus* seedlings was also markedly greater in the no-grazing treatments compared to the control plots. However, RHI of both seedling species in the G-S- treatment was not statistically greater than those in the G+S+ plots, which is a strong indication that unless shade is provided, fencing alone cannot guarantee the establishment of *L. scoparium* and *O. leptophyllus* in these areas. A 37-year study on the recovery of a short-tussock site in Wairau catchment, Marlborough, showed that reduced levels of grazing prompted significant recovery of native shrubs, tall tussocks, and herbs. However, the density of invasive exotic species (*Hieracium* among others) also increased and tended to become the dominant cover after a few years (Rose et al., 2004). Although reductions in mammalian herbivore populations have led to marked recovery of native tree and shrub species in different forest types across New Zealand (Norway rats in Allen et al, 1994; rats and possums in Wilson et al., 2003; and ungulates in Wright et al. 2012), plants' responses to herbivory vary with composition and environment. Allen et al. (1995) observed that perennials increased six years after cessation of grazing in a semi-arid grassland, but yearly variation in composition was at least as great as that between grazed and ungrazed plots. In this context, the tendency is for invasive weeds and herb species to increase in density in the absence of grazing on the Degraded Short Tussock sites since the composition and structure of native plant species pose few effective barriers to establishment of exotic plants (Rose et al., 1998; Rose & Frampton, 1999). The present research did not investigate treatment effects on exotic weed infestation and their density across the Degraded Short Tussock study sites, but rather on whether general herbivory could be an issue for native seedling establishment in the area. Consequently, it is only possible to assume with certainty that competition with exotic weeds will increase with exclusion of herbivory, although it is a possibility.

Soil moisture levels did not seem to respond to grazing or its removal, but were more closely linked to the existence/absence of shade, similarly to what Payne and Norton (2011) detected at the same site in a different experiment. Thus, it cannot be presumed that the higher probabilities of survival and growth in the no-grazing treatments were somehow related to changes to soil water levels in these plots. It is worth noting that in January-2014, the estimated soil water content in the grazing-and-shade (G+S+) treatment was higher than in the no grazing-and-shade (G-S+) plots. This small discrepancy in soil moisture between these two treatments was only detected in this period and may be related to the denser exotic weed cover in the G-S+ plots (personal observation), especially within the 15-20 cm soil depth where soil samples were collected. Dalley et al. (2006) found that weed presence reduced soil moisture in the 0-18 cm soil depth in early summer (June), further decreasing soil moisture within deeper layers later in the summer (August). Broadleaf weeds such as *Hieracium* spp., a widespread exotic plant species commonly found in the short-tussock grasslands around New Zealand (Fan & Harris, 1996) and dominant in the Irrigation and Grazing sites, can extract more moisture from soil profile (DiTomaso, 2000). Potentially, herbivory may have the indirect, yet positive, impact on soil water content and, as a result, reduce plant competition for soil water, especially in the summer, when this resource becomes scarcer.

6. Conclusions and Implications of the Research for Practical Restoration Ecology

Biological communities all have the self-regenerating capacity through ecological succession to overcome changes in ecological processes following a disturbance event, which enables the entire system to perpetuate on the landscape. Ecological succession continuously takes place after the disturbance through the replacement or recovery of the lost species, or by repairing ecological functions, in order to restore the natural balance between the biota and the physical environment (Johnson & Miyanishi, 2010). The time length for post-succession regeneration to occur will depend on the nature, duration, and intensity of the environmental impact (Hobbs & Norton, 1996), as well as on the ecosystem's capacity to absorb impact and reorganize itself (Folke et al., 2004), also known as resilience (Lugo, 1988). However, ecological succession can be extremely slow and the original biological community may never return to its historic state when disturbances break biotic and abiotic interactions, and permanently affect certain system components (Hobbs & Harris, 2001; Allen et al., 2006), thus creating a new ecological state which no longer supports the original biota (Mark & McLennan, 2005). Where this has occurred as a result of anthropogenic factors, the ecosystem is often classified as degraded because the disturbance event pushed specific ecological functions or processes over a threshold that, unless adequately managed, will result in the replacement of the original biological community by a different assemblage of species, called an alternative state or "novel ecosystem" (Hobbs et al., 2006). Consequently, researchers and restorationists are now incorporating the state-and-transition models for ecological restoration to understand how present environmental factors differ from the original conditions, what ecological thresholds have been breached by disturbance events, and how to manipulate these factors into fitting the native species' requirements to recolonize the landscape (Pyke & Knick, 2005; Walker et al., 2009a; Ammondt & Litton, 2012). Thence, ecological restoration plans need to integrate reintroduction of the native biota (Carter & Newbery, 2004; Costa & DeLotelle, 2006) with modifications to the physical environment (Tang et al., 2009), based on a good understanding of the history and characteristics of the disturbance (Walker et al., 2009a) in order to maximize restoration success. Planning ecological restoration efforts for New Zealand's dryland ecosystems should be no different. Therefore, the goal of the present research was to determine which ecological thresholds have been crossed and, consequently, become barriers to the reintroduction of the

native woody tree species on abandoned farmlands. The research involved the manipulation of specific abiotic (e.g. direct solar radiation and water stress) and biotic factors (e.g. presence of exotic plant species and herbivores) previously hypothesized as key factors hindering restoration efforts in the areas based on the knowledge about past land use practices.

New Zealand's dryland zone has progressively lost its natural vegetation cover since the arrival of Polynesian/Maori settlers *c.a* 700 years ago, when the woody strata was probably reduced to shrub and grasslands through burning (McGlone et al., 2001). Degradation of the native grassland into exotic herbfields continued with the arrival of Europeans who introduced their agricultural and pastoral practices, along with mammals and plant species to improve pasture quality for grazing animals. Introduction of mammals contributed to the degradation of New Zealand's native ecosystems by exposing the flora to unprecedented herbivory and fungal and/or bacterial diseases. Deforestation, agriculture, pastoral practices and exotic species invasions did not affect the biotic elements only, but also soil physical and chemical properties, thus hindering restoration of the native vegetation even years after the activities have ceased. Currently, around 30% of the native vegetation remains in the dryland zone, but most of this is limited to higher altitudes and steep slopes where agriculture and pastoralism are more difficult, and <2% is legally protected (Walker et al., 2009b). Restoration of New Zealand's dryland areas is urgently required to address this habitat loss and the present research has shown how human intervention can best facilitate restoration of woody vegetation.

The direct and constant exposure of young plants to solar radiation was found as the main environmental factor that needs to be managed to improve native seedling establishment and growth on the study sites. The creation of shelter through shade cloths most likely acts as a proxy for the historic woody vegetation cover that would have been present in these areas. The shade provided reduces water stress and improves the microclimate, therefore creating a more advantageous environment for native seedlings to develop and survive in the long term without the need to implement an irrigation system, for instance, or other expensive methods. In the one trial where it was tested, irrigation did not prove essential for *Leptospermum scoparium* and *Ozothamnus leptophyllus* seedlings used in this research. Supplemental water was more favorable than the current environmental conditions, however it was most effective when combined with shade. The better responses of the native seedlings under the shade cloths may

also have been related to improvements in the soil's physical conditions; more specifically, reduced soil compaction due to lower evapotranspiration and, consequently, improved soil aeration for better development of the seedlings' root system. Higher growth and survival rates of seedlings in the shaded treatments would have been a direct response of higher photosynthetic efficiency, which is responsible for plant production; hence, plant growth. Additionally, shade cloth shelters probably played an important role in protecting seedlings from extremely cold temperatures and frost due to a more moderated microclimate under the shade cloth, and as a physical barrier from snowfall in winter.

Grass removal, although varying in effectiveness, proved necessary for restoration efforts at the sites where a rank grass sward was dominant (Tiromoana Bush, The Willows Reserve, and Dierickx Farm). As discussed above, shade was the most important requirement for guaranteeing seedling establishment in the Rank Grass experiments and not surprisingly, grass removal methods provided the best results when combined with shade. Grass removal did not seem to influence soil water levels, but its positive effects were more likely correlated to the reduced plant competition between exotic grasses and the native seedlings for soil resources. Consequently, the choice of grass removal method needs to be thoroughly considered before being put into practice, as some methods may have undesirable effects on the restoration plantings, as observed in the poor performance of the native seedlings in the mulch-no-shade treatments at the Rank Grass sites. The mulch used for the Rank Grass experiments was effective in elevating soil moisture, smothering the exotic grasses and preventing re-infestation of the plots. However, unless combined with shade cloths, the growth of native seedlings was hampered most likely because of a thermal trap created between the soil surface and the black plastic cover used as part of the mulch treatment (Marushia & Allen, 2011). The heat probably increased microbial activity under the mat that, combined with higher soil moisture, led to high seedling mortality by anoxia (Romic et al., 2008; Pfeifer et al., 2014).

The Grazing experiment on the Degraded Short Tussock sites in the Mackenzie Basin highlighted the importance of fencing primarily for the establishment of *O. leptophyllus* seedlings and *L. scoparium* seedlings, the latter mostly being a "victim of opportunity", even though these species are regarded in the literature as unpalatable to herbivores. Therefore, fencing, along with some form of shelter, should be regarded as a valuable restoration tool for

areas that are infested with rabbits and hares, and still have some influence from domestic grazing animals (sheep). Competition with exotic weeds for resources is expected to decrease if abiotic factors and herbivores are dealt with, thus improving environmental conditions for native plants to invest more energy in growth instead of in defense mechanisms. Unstressed plants are more likely to grow continuously and guarantee the success of restoration efforts. The use of defense mechanisms to dissipate excessive energy due to high irradiance and temperatures, and/or to maintain CO_2 levels in the leaves under water stress, can increase the chances of survival for the seedlings growing in adverse environmental conditions, but not without high costs for plant development (Baltzer et al., 2005). High photosynthetic and water use efficiencies are sustained by high metabolic rates to compensate for the lower CO_2 diffusion due to stomata closure in water stress and high irradiance conditions (Terwilliger et al., 2001; Reddy et al., 2004) resulting in slower growth rates (Caldwell et al., 1998; de Gouvenain et al., 2007). If the effects of high irradiance on soil and air temperatures, soil moisture, and soil aeration can be reduced, and herbivores are removed, native seedlings will grow better, faster, and be more competitive.

In summary, the results obtained in the Rank Grass and Degraded Short Tussock trials have answered the general hypotheses raised in the beginning of the experiments:

- Water availability is a limiting factor to the establishment of native woody species in the dryland zone, and its shortage is intensified by the exposure of the soil to direct sun light and the presence of exotic grass and weed species;
- The use of shelters was effective for the development of the native seedlings as they were protected from weather elements, essentially direct solar radiation and high wind. The native seedlings benefitted from the more moderated microclimate underneath the shade cloths and increased soil moisture which led to a higher probability of seedling survival and growth under the shaded treatments;
- Creation of shelter and the removal of exotic grass also had a positive impact on native seedling establishment and growth likely due to reduced soil compaction and improvements in soil aeration for better development of plant roots;

- Competition between native and exotic plants for soil resources and light was reduced by the grass removal treatments, which consequently improved the chances of survival and development of the native seedlings in the areas.

Other observations based on the present study are considered important for ecological restoration plans for areas with similar environmental characteristics as those identified in this research. These are timing, active planting of different species, conservationists and farmers working mutually, and more comprehensive field measurements.

6.1 Time is of the Essence

Restoration of degraded ecosystems is a priority for land management in many different biomes, but is especially important in drylands, as they are being destroyed quickly throughout the globe (Bainbridge, 2012; Mueller et al., 2014). The rapid modifications of natural landscapes to "novel ecosystems", mostly caused by anthropogenic disturbances and climate change (Hobbs et al., 2006; Seastedt et al., 2008), are reducing the likelihood of restoring degraded landscapes back to their original or historic state (Hobbs & Cramer, 2008). Therefore, modern restoration strategies must include specific strategies to manage the various environmental factors that are involved in maintaining and propagating the degraded state of an ecosystem (e.g. invasive species, soil compaction and/or toxicity, and water deficit). Planting of native species, primarily woody species, is fundamental to initiate the process of restoration, as re-introduced species stimulate the recovery of the ecosystem's structure, composition, and functions, at the same time that further degradation is halted (Cortina & Maestre, 2005; Vallejo et al., 2006). Choosing the appropriate period of the year to plant or seed is critical and should take place when plant metabolism is low (Anderson & Ostler, 2002). For New Zealand's dryland natives, this should be early spring, when soils are still moist, but temperatures are increasing towards a more suitable range, and seedlings may take advantage of the supplemental water to survive through the dry, hot summer.

6.2 Active Planting and Framework Species

Plant-plant interactions, resulting from the net output of positive and negative interactions, are crucial for ecosystem composition, structure and dynamics in drylands (Whitford, 2002).

Because of their fast-growing and seral characteristics, these nurse plants can quickly provide shade for more shade-tolerant species and facilitate ecological succession (Lugo, 1997; Blakesley et al., 2002a; Widmann et al., 2005b). It is important to plant different species to avoid problems derived from monospecific plantations such as fire propagation (Doerr et al., 1998) or soil impoverishment (Maestre & Cortina, 2004). Additionally, different plant species increase the diversity and heterogeneity of the restored plant communities (Gómez-Aparicio et al., 2004). Soil resources and microclimate have certain spatial patterns that are highly related to the spatial distribution of plant associations (Halvorson et al., 1995; Moro et al., 1997), and this relationship promotes the existence of different niches as the number of plant species increases (Pugnaire et al., 1996). More niche heterogeneity provided by varying species of nurse plants increases habitat availability and, along with improvements in microclimate, provide more adequate environmental conditions for re-introduction of native plant and animal species (Callaway & Walker, 1997). Actively planting trees is likely to be the most effective for short-tussock grassland restoration where trees can control erosion as trees grow taller and, perhaps, reduce hawkweed dominance in the long term (Walker et al., 2009b; Syrett et al., 2012).

Another alternative for a "jump start" for ecological restoration in severely degraded areas is the planting of exotic species. Although it is a controversial conservation technique (D'Antonio & Meyerson, 2002), the use of exotic plant species as nurse plants can assist restoration in dryland areas in New Zealand (Walker et al., 2009b; Carswell et al., 2012; Burrows et al., 2015) by preparing the habitat (e.g. nitrogen-fixing, decreased evapotranspiration) for reintroduced native plant species (Parrotta et al., 1997; Parrotta, 1999). The implementation of shade cloth shelters can be costly, especially when attempted at a larger scale than a research trial, and logistically impractical in some situations because of topography and distances that incur high costs of transportation and labor. In such cases, shelter can be provided by certain fast-growing exotic species already present in the area, such as Scotch broom (*Cytisus scoparius*, Burrows et al., 2015), sweet briar (*Rosa rubiginosa*, Walker et al., 2003a), and gorse (*Ulex europaeus*, Sullivan et al., 2007 and Williams and Karl, 2002), common invasive shrubs in New Zealand, that can therefore be used as nurse plants for the native seedlings. Walker et al. (2014) observed that secondary exotic-shrubland vegetation did support a variety of indigenous herb and shrub species in a South Island dryland area. Other recent studies in Canada and in New Zealand's North

Island show that plantation forests allow the establishment of high concentrations of native tree species in the understory (Boothroyd-Roberts et al., 2013; Forbes et al., 2014). The results of these aforementioned experiments, therefore, contradict the species-displacement hypothesis suggested by (Rogers et al., 2005), which states that specialist light-demanding native plant species would be displaced by more generalist exotic woody and grass species during succession, and that native plants would be unable to establish under the exotic secondary vegetation cover. The results obtained by Walker et al. (2014), however, showed no displacement or loss of native grassland-specialist species during succession within an exotic-shrubland landscape near Dunedin, in the South Island. Their results are relevant for restoration efforts in degraded dryland areas in New Zealand, such as those analyzed in this thesis, since they provide evidence that native plants can reestablish and become part of the succession process in areas that are currently covered by exotic grass and woody species. Exotic trees may be removed later on through sustainable forest management practices (Norton & Reid, 2013) when native plants have reached a certain height and they no longer require shelter to continue growing for ecological succession to carry on with minimal or no human assistance. However, the use of exotic nurse plants needs to be implemented with caution and consideration needs to be given to the weediness of these species (Lugo, 1997; Shackelford et al., 2013).

6.3 Farmers are not Foes

Stimulating farmers to plant native species on farmland can only lead to positive outcomes to the economy and the environment (Norton & Reid, 2013), through creating shelterbelts to protect livestock and agricultural crops, at the same time enhancing biodiversity conservation by reducing ecological fragmentation and creating habitat for native fauna (Norton & Miller, 2000; Tompkins, 2010). Native plant species on active farmlands can also have the beneficial effect of protecting crops from pests and diseases by attracting the attention of potentially harmful insects towards them (Landis et al., 2012; James et al., 2014). Increasing the varieties of plant species increases the number of herbivorous insect species and potential prey for generalist predators (Davidson & Howlett, 2010).

6.4 Recommendations for Future Studies

Lastly, the results of the present study have shown that restoration efforts in North Canterbury and Mackenzie Basin areas are not simple, but can be achieved once the specific ecological factors preventing restoration of the plant community are identified and managed. In the case of the study sites in particular, shade was fundamental for better seedling establishment and growth, probably due to its influence on soil water availability and the plants' vulnerability to herbivory and the presence of invasive plant species. Nevertheless, the results also indicate that future research should obtain morphological and other types of physiological data, such as stomatal conductance and gas exchange, in order to verify some of the new hypotheses raised after analyzing the results. Measuring a plants' dry biomass, for instance, would determine whether the native seedlings did use biomass reallocation strategies to cope with harsh environmental conditions. Leaf area ratio and pigment (anthocyanins) analysis of leaves would show another possible defense mechanism of seedlings to avoid photoinhibition; gas exchange or stomatal conductance measurements combined with carbon isotope signature would help determine which water use strategy the plants have, etc. Trees and grasses respond differently to environmental factors due to their differing niches (February et al., 2013a; Kulmatiski & Beard, 2013), and therefore a study that could assess the responses of both native and invasive plant species to environmental stress would provide a more comprehensive understanding of the ecological interactions between these different plant forms and the ecosystem. Research that includes broader data collection of plants' responses may lead to more cost-effective restoration efforts targeted at specific areas and plant communities, and increase restoration success in the future.

7. References

Abdollahi L, Schjønning P, Elmholt S, and Munkholm LJ (2014) The effects of organic matter application and intensive tillage and traffic on soil structure formation and stability. Soil and Tillage Research **136**:28-37

Adams III WW, Muller O, Cohu CM, and Demmig-Adams B (2013) May photoinhibition be a consequence, rather than a cause, of limited plant productivity? Photosynth Res **117**:31-44

Adams III WW, Zarter CR, Mueh KE, and Demmig-Adams B (2006) Energy dissipation and photoinhibition: a continuum of photoprotection. Pages 49-64 In: Photoprotection, photoinhibition, gene regulation, and environment. Springer

Adir N, Zer H, Shochat S, and Ohad I (2003) Photoinhibition–a historical perspective. Photosynth Res **76**:343-370

Adiredjo A, Navaud O, Lamaze T, and Grieu P (2014) Leaf Carbon Isotope Discrimination as an Accurate Indicator of Water-Use Efficiency in Sunflower Genotypes Subjected to Five Stable Soil Water Contents. Journal of Agronomy and Crop Science **200**:416-424

Aliyu B, Adamu H, Moltchanova E, Forget PM, and Chapman H (2014) The Interplay of Habitat and Seed Type on Scatterhoarding Behavior in a Fragmented Afromontane Forest Landscape. Biotropica **46**:264-267

Allen R, Duncan R, and Lee W (2006) Updated perspective on biological invasions in New Zealand. Pages 435-451 In: Biological Invasions in New Zealand. Springer

Allen R, Lee W, and Rance B (1994) Regeneration in indigenous forest after eradication of Norway rats, Breaksea Island, New Zealand. New Zealand Journal of Botany **32**:429-439

Allen R, Wilson JB, and Mason C (1995) Vegetation change following exclusion of grazing animals in depleted grassland, Central Otago, New Zealand. Journal of Vegetation Science **6**:615-626

Allen RB, Partridge TR, Lee WG, and Efford M (1992) Ecology of *Kunzea ericoides* (A. Rich.) J. Thompson (kanuka) in east Otago, New Zealand. New Zealand Journal of Botany **30**:135-149

Ammondt SA, and Litton CM (2012) Competition between Native Hawaiian Plants and the Invasive Grass *Megathyrsus maximus*: Implications of Functional Diversity for Ecological Restoration. Restoration Ecology **20**:638-646

Anderson DC, and Ostler WK (2002) Revegetation of Degraded Lands at U.S. Department of Energy and U.S. Department of Defense Installations: Strategies and Successes. Arid Land Research and Management **16**:197-212

Arihafa A (2008) The Use of a Geographic Information System (GIS) in Determining the Past and Present Vegetation Pattern of Tiromoana Bush, Northern Canterbury, 1950-2005. University of Canterbury, Christchurch, New Zealand

Arnold G, Abensperg-Traun M, Hobbs RJ, Steven D, Atkins L, Viveen J, and Gutter D (1999) Recovery of shrubland communities on abandoned farmland in southwestern Australia: soils, plants, birds and arthropods. Pacific Conservation Biology **5**:163

Atkin O, Loveys B, Atkinson L, and Pons T (2006) Phenotypic plasticity and growth temperature: understanding interspecific variability. J Exp Bot **57**:267-281

Atkinson I (2006) Introduced mammals in a new environment. Pages 49-66 In: Biological Invasions in New Zealand. Springer

Aweto A (1981) Secondary succession and soil fertility restoration in south-western Nigeria: II. Soil fertility restoration. The Journal of Ecology:609-614

Bainbridge DA. (2012) A guide for desert and dryland restoration: new hope for arid lands. Island Press

Baker NR (2008) Chlorophyll fluorescence: a probe of photosynthesis in vivo. Annu Rev Plant Biol **59**:89-113

Ballaré CL, Scopel AL, Stapleton AE, and Yanovsky MJ (1996) Solar ultraviolet-B radiation affects seedling emergence, DNA integrity, plant morphology, growth rate, and attractiveness to herbivore insects in *Datura ferox*. Plant Physiol **112**:161-170

Baltzer JL, Thomas SC, Nilus R, and Burslem DFRP (2005) Edaphic Specialization in Tropical Trees: Physiological Correlates and Responses to Reciprocal Transplantation. Ecology **86**:3063-3077

Banerjee MJ, Gerhart VJ, and Glenn EP (2006) Native Plant Regeneration on Abandoned Desert Farmland: Effects of Irrigation, Soil Preparation, and Amendments on Seedling Establishment. Restoration Ecology **14**:339-348

Bannister P (2003) Are frost hardiness ratings useful predictors of frost damage in the field? A test using damage records from the severe frost in South Otago and Southland, New Zealand, July 1996. New Zealand Journal of Botany **41**:555-569

Baraza E, Zamora R, Hódar JA, and Larsson S (2006) Conditional Outcomes in Plant-Herbivore Interactions: Neighbours Matter. Oikos **113**:148-156

Barbour MM, Mcdowell NG, Tcherkez G, Bickford CP, and Hanson DT (2007) A new measurement technique reveals rapid post-illumination changes in the carbon isotope composition of leaf-respired CO2. Plant, Cell & Environment **30**:469-482

Barclay A, and Crawford R (1982) Plant growth and survival under strict anaerobiosis. J Exp Bot **33**:541-549

Bardet J-P. (1997) Experimental soil mechanics. Prentice Hall Upper Saddle River, NJ,

Baumeister D, and Callaway RM (2006) Facilitation by *Pinus flexilis* during succession: A hierarchy of mechanisms benefits other plant species. Ecology **87**:1816-1830

Bee JN, Kunstler G, and Coomes DA (2007) Resistance and resilience of New Zealand tree species to browsing. Journal of Ecology **95**:1014-1026

Benayas JMR, Navarro J, Espigares T, Nicolau JM, and Zavala MA (2005) Effects of artificial shading and weed mowing in reforestation of Mediterranean abandoned cropland with contrasting *Quercus* species. Forest Ecology and Management **212**:302-314

Bilotta G, Brazier R, and Haygarth P (2007) The impacts of grazing animals on the quality of soils, vegetation, and surface waters in intensively managed grasslands. Advances in Agronomy **94**:237-280

Binkley D, and Fisher RF. (2013) Ecology and Management of Forest Soils. John Wiley & Sons, Ltd.

Blakesley D, Elliott S, Kuarak C, Navakitbumrung P, Zangkum S, and Anusarnsunthorn V (2002a) Propagating framework tree species to restore seasonally dry tropical forest: implications of seasonal seed dispersal and dormancy. Forest Ecology and Management **164**:31-38

Blakesley D, Elliott S, Kuarak C, Navakitbumrung P, Zangkumb S, and Anusarnsunthorn V (2002b) Propagating framework tree species to restore seasonally dry tropical forest: implications of seasonal seed dispersal and dormancy. Forest Ecology and Management **164**:31-38

Bohnert HJ, and Sheveleva E (1998) Plant stress adaptations—making metabolism move. Current Opinion in Plant Biology **1**:267-274

Bond WJ, Dickinson KJ, and Mark AF (2004) What limits the spread of fire-dependent vegetation? Evidence from geographic variation of serotiny in a New Zealand shrub. Global Ecology and Biogeography **13**:115-127

Boothroyd-Roberts K, Gagnon D, and Truax B (2013) Can hybrid poplar plantations accelerate the restoration of forest understory attributes on abandoned fields? Forest Ecology and Management **287**:77-89

Boswell C, and Espie P (1998) Uptake of moisture and nutrients by *Hieracium pilosell*a and effects on soil in a dry sub-humid grassland. New Zealand Journal of Agricultural Research **41**:251-261

Boyden S, Binkley D, and Stape JL (2008) Competition among *Eucalyptus* trees depends on genetic variation and resource supply. Ecology **89**:2850-2859

Bradbury M, and Baker NR (1984) A quantitative determination of photochemical and non-photochemical quenching during the slow phase of the chlorophyll fluorescence induction curve of bean leaves. Biochimica et Biophysica Acta (BBA)-Bioenergetics **765**:275-281

Bradshaw A (1997) Restoration of mined lands using natural processes. Ecological Engineering **8**:255-269

Brand DG (1991) The establishment of boreal and sub-boreal conifer plantations: an integrated analysis of environmental conditions and seedling growth. Forest Science **37**:68-100

Briske DD, Fuhlendorf SD, and Smeins FE (2003) Vegetation Dynamics on Rangelands: A Critique of the Current Paradigms. Journal of Applied Ecology **40**:601-614

Brooking T, Hodge R, and Wood V (2002) The grasslands revolution reconsidered. Pawson, e.; Brooking, T.(eds): environmental histories of New Zealand. Oxford University Press, Melbourne:169-182

Brooks ML, D'antonio CM, Richardson DM, Grace JB, Keeley JE, Ditomaso JM, Hobbs RJ, Pellant M, and Pyke D (2004) Effects of invasive alien plants on fire regimes. BioScience **54**:677-688

Brown S, and Lugo AE (1994) Rehabilitation of tropical lands: a key to sustaining development. Restoration Ecology **2**:97-111

Bryson CT, and Carter R (2009) Biology of Pathways for Invasive Weeds

Bunker DE, and Carson WP (2005) Drought stress and tropical forest woody seedlings: effect on community structure and composition. Journal of Ecology **93**:794-806

Burke IC, Lauenroth WK, Vinton MA, Hook PB, Kelly RH, Epstein HE, Aguiar MR, Robles MD, Aguilera MO, and Murphy KL (1998) Plant-soil interactions in temperate grasslands. Pages 121-143 In: Plant-induced soil changes: Processes and feedbacks. Springer

Burrell J (1965) Ecology of Leptospermum in Otago. New Zealand Journal of Botany **3**:3-16

Burrows L, Cieraad E, and Head N (2015) Scotch broom facilitates indigenous tree and shrub germination and establishment in dryland New Zealand. New Zealand Journal of Ecology **39**:0-0

Butler WL (1978) Energy distribution in the photochemical apparatus of photosynthesis. Annual Review of Plant Physiology **29**:345-378

Byers JE, and Noonburg EG (2003) Scale dependent effects of biotic resistance to biological invasion. Ecology **84**:1428-1433

Cabin RJ, Weller SG, Lorence DH, Cordell S, J.Hadway L, Montgomery R, Goo D, and Urakami A (2002) Effects of Light, Alien Grass, and Native Species Additions on Hawaiian Dry Forest Restoration Ecological Applications **12**:1595-1610

Caldwell MM (1970) Plant Gas exchange at High Wind Speeds. Plant Physiol **46**:535-537

Caldwell MM, Bjhn LO, Bornman JF, Flint SD, G. Kulandaivelu, Teramura AH, and Tevini M (1998) Effects of increased solar ultraviolet radiation on terrestrial ecosystems. Journal of Photochemistry and Photobiology B: Biology **46**:40-52

Caldwell MM, Bornman JF, Ballare CL, Flint SD, and Kulandaivelu G (2007) Terrestrial ecosystems, increased solar ultraviolet radiation, and interactions with other climate change factors. Photochem Photobiol Sci **6**:252-266

Caldwell TG, Mcdonald EV, and Young MH (2009) The seedbed microclimate and active revegetation of disturbed lands in the Mojave Desert. Journal of Arid Environments **73**:563-573

Callaway RM (1995) Positive Interactions among Plants. Botanical Review **61**:306-349

Callaway RM, and Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology **78**:1958-1965

Campbell D (2010) Factors Limiting Natural Forest Regeneration in a Nigerian Montane Grassland. University of Canterbury, Christchurch, New Zealand

Carswell FE, Burrows LE, Hall GM, Mason NW, and Allen RB (2012) Carbon and plant diversity gain during 200 years of woody succession in lowland New Zealand. New Zealand Journal of Ecology **36**:191

Carter I, and Newbery P (2004) Reintroduction as a tool for population recovery of farmland birds. Ibis **146**:221-229

Catoni R, and Gratani L (2014) Variations in leaf respiration and photosynthesis ratio in response to air temperature and water availability among Mediterranean evergreen species. Journal of Arid Environments **102**:82-88

Causton D (1991) Plant growth analysis: the variability of relative growth rate within a sample. Annals of Botany **67**:137-144

Cavanaugh ML, Kurc SA, and Scott RL (2011) Evapotranspiration partitioning in semiarid shrubland ecosystems: a two-site evaluation of soil moisture control on transpiration. Ecohydrology **4**:671-681

Cernusak LA, Aranda J, Marshall JD, and Winter K (2007) Large variation in whole-plant water-use efficiency among tropical tree species. New Phytologist **173**:294-305

Cernusak LA, Hutley LB, Beringer J, Holtum JA, and Turner BL (2011) Photosynthetic physiology of eucalypts along a sub-continental rainfall gradient in northern Australia. Agricultural and Forest Meteorology **151**:1462-1470

Cernusak LA, Ubierna N, Winter K, Holtum JA, Marshall JD, and Farquhar GD (2013) Environmental and physiological determinants of carbon isotope discrimination in terrestrial plants. New Phytologist **200**:950-965

Chaves MM, Flexas J, and Pinheiro C (2009) Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann Bot **103**:551-560

Chaves MM, Maroco JP, and Pereira JS (2003) Understanding plant responses to drought—from genes to the whole plant. Functional Plant Biology **30**:239-264

Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osório ML, Carvalho I, Faria T, and Pinheiro C (2002) How plants cope with water stress in the field? Photosynthesis and growth. Annals of Botany **89**:907-916

Chib S, and Greenberg E (1995) Understanding the metropolis-hastings algorithm. The American Statistician **49**:327-335

Chiu CF, Yan WM, and Yuen K-V (2012) Estimation of water retention curve of granular soils from particle-size distribution — a Bayesian probabilistic approach. Canadian Geotechnical Journal **49**:1024-1035

Christian R, Kelly D, and Turnbull MH (2006) The architecture of New Zealand's divaricate shrubs in relation to light adaptation. New Zealand Journal of Botany **44**:171-186

Cieraad E, Burrows L, Monks A, and Walker S (2015) Woody native and exotic species respond differently to New Zealand dryland soil nutrient and moisture gradients. New Zealand Journal of Ecology **39**:0-0

Clary J, Save R, Biel C, and Herralde FD (2004) Water relations in competitive interactions of Mediterranean grasses and shrubs. Annals of Applied Biology **144**:149-155

Cleland RE, Melis A, and Neale PJ (1986) Mechanism of photoinhibition: photochemical reaction center inactivation in system II of chloroplasts. Pages 77-86 In: Current topics in photosynthesis. Springer

Clements FE. (1916) Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington,

Clout MN, and Hay JR (1989) The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. New Zealand Journal of Ecology **12**:27-33

Connor HE, and Edgar E (1987) Name changes in the indigenous New Zealand flora, 1960–1986 and Nomina Nova IV, 1983–1986. New Zealand Journal of Botany **25**:115-171

Cooke SJ, and Suski CD (2008) Ecological Restoration and Physiology: An Overdue Integration. BioScience **58**:957-968

Coomes DA, and Grubb PJ (2000) Impacts of Root Competition in Forests and Woodlands: A Theoretical Framework and Review of Experiments. Ecological Monographs **70**:171-207

Cooper DJ, Merritt DM, Andersen DC, and Chimner RA (1999) Factors controlling the establishment of fremont cottonwood seedlings on the upper green river, USA. Regulated Rivers: Research & Management **15**:419-440

Coopman RE, Jara JC, Escobar R, Corcuera LJ, and Bravo LA (2010) Genotypic variation in morphology and freezing resistance of *Eucalyptus globulus* seedlings subjected to drought hardening in nursery. Electronic Journal of Biotechnology **13**:5-6

Cordell S, and Sandquist DR (2008) The impact of an invasive African bunchgrass (*Pennisetum setaceum*) on water availability and productivity of canopy trees within a tropical dry forest in Hawaii. Functional Ecology **22**:1008-1017

Cornic G, and Fresneau C (2002) Photosynthetic carbon reduction and carbon oxidation cycles are the main electron sinks for photosystem II activity during a mild drought. Annals of Botany **89**:887-894

Cortina J, and Maestre FT (2005) Plant Effects on Soils in Drylands: Implications for Community Dynamics and Ecosystem Restoration. Pages 85-118 In: Binkley D and Menyailo O, (eds) Tree Species Effects on Soils: Implications for Global Change. Springer, Netherlands

Costa R, and Delotelle RS (2006) Reintroduction of Fauna to Longleaf Pine Ecosystems: Opportunities and Challenges. Pages 335-376 In: Jose S, Jokela EJ and Miller DL, (eds) The Longleaf Pine Ecosystem. Springer New York, New York

Craine J, and Lee W (2003) Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. Oecologia **134**:471-478

Craine J, Lee W, and Walker S (2006) The context of plant invasions in New Zealand: evolutionary history and novel niches. Pages 167-177 In: Biological Invasions in New Zealand. Springer

Crawford RM (2012) Long-Term Anoxia Tolerance in Flowering Plants. Pages 219-246 In: Anoxia. Springer

D'antonio C, and Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology **10**:703-713

D'antonio CM, Hughes RF, Mack M, Hitchcock D, and Vitousek PM (1998) The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. Journal of Vegetation Science **9**:699-712

D'antonio CM, and Vitousek PM (1992) Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change. Annual Review of Ecology and Systematics **23**:63-87

Dalley CD, Bernards ML, and Kells JJ (2006) Effect of Weed Removal Timing and Row Spacing on Soil Moisture in Corn (*Zea mays*). Weed Technology **20**:399-409

Das A, Lal R, Patel DP, Idapuganti RG, Layek J, Ngachan SV, Ghosh PK, Bordoloi J, and Kumar M (2014) Effects of tillage and biomass on soil quality and productivity of lowland rice cultivation by small scale farmers in North Eastern India. Soil and Tillage Research **143**:50-58

Davidson M, and Howlett B (2010) Hedging our bets: choosing hedgerow plants to enhance beneficial insects to optimise crop pollination and pest management on Canterbury farms

Davis MA, and Pelsor M (2001) Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters **4**:421-428

Dawson J, Lucas R, Connor J, and Brownsey PJ. (2011) New Zealand's native trees. Craig Potton,

De Gouvenain RC, Kobe RK, and Silander JA (2007) Partitioning of understorey light and dry-season soil moisture gradients among seedlings of four rain-forest tree species in Madagascar. Journal of Tropical Ecology **23**:569

Dexter A (2004) Soil physical quality: Part I. Theory, effects of soil texture, density, and organic matter, and effects on root growth. Geoderma **120**:201-214

Diefendorf AF, Mueller KE, Wing SL, Koch PL, and Freeman KH (2010) Global patterns in leaf 13C discrimination and implications for studies of past and future climate. Proceedings of the National Academy of Sciences **107**:5738-5743

Ditomaso JM (2000) Invasive Weeds in Rangelands: Species, Impacts, and Management. Weed Science **48**:255-265

Dobson AP, Bradshaw A, and Baker AÁ (1997) Hopes for the future: restoration ecology and conservation biology. Science **277**:515-522

Doerr SH, Shakesby RA, and Walsh RP (1998) Spatial variability of soil hydrophobicity in fire-prone eucalyptus and pine forests, Portugal. Soil Science **163**:313-324

Drew MC (1997) Oxygen deficiency and root metabolism: Injury and Acclimation Under Hypoxia and Anoxia. Annu. Rev. Plant Physiol. Plant Mol. Biol. **48**:223-250

Dulamsuren C, and Hauck M (2008) Spatial and seasonal variation of climate on steppe slopes of the northern Mongolian mountain taiga. Grassland Science **54**:217-230

Ehleringer J, Hall A, and Farquhar G (1993) Carbon and water relations in desert plants: an isotopic perspective. Pages 155-172 Stable isotopes and plant carbon-water relations. Academic Press Inc.

Ehleringer JR, and Cooper TA (1988) Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia **76**:562-566

Ehleringer JR, and Sandquist DR (2006) Ecophysiological constraints on plant responses in a restoration setting. Foundations of Restoration Ecology **42**

Eiten G (1972) The Cerrado Vegetation of Brazil. Botanical Review **38**:201-341

Ellison AM (2004) Bayesian inference in ecology. Ecology Letters **7**:509-520

Elmore CL, Stapleton JJ, Bell CE, and Devay JE. (1997) Soil solarization: a method for controlling diseases, nematodes and weeds. University of California, California, USA

Engelbrecht BM, Dalling JW, Pearson TR, Wolf RL, Galvez DA, Koehler T, Tyree MT, and Kursar TA (2006) Short dry spells in the wet season increase mortality of tropical pioneer seedlings. Oecologia **148**:258-269

Erdmann B, and Wiedenroth E (1988) Changes in the root system of wheat seedlings following root anaerobiosis: III. Oxygen concentration in the roots. Ann Bot **62**:277-286

Esler AE, and Astridge SJ (1974) Tea tree (*Leptospermum*) communities of the Waitakere Range, Auckland, New Zealand. New Zealand Journal of Botany **12**:485-501

Etzenhouser MJ, Owens MK, Spalinger DE, and Murden SB (1998) Foraging behavior of browsing ruminants in a heterogeneous landscape. Landscape Ecology **13**:55-64

Evans GC. (1972) The quantitative analysis of plant growth. Univ of California Press,

Fan J, and Harris W (1996) Effects of soil fertility level and cutting frequency on interference among *Hieracium pilosella*, *H. praealtum*, *Rumex acetosella*, and *Festuca novae-zelandiae*. New Zealand Journal of Agricultural Research **39**:1-32

Faria T, García-Plazaola J, Abadia A, Cerasoli S, Pereira J, and Chaves M (1996) Diurnal changes in photoprotective mechanisms in leaves of cork oak (*Quercus suber*) during summer. Tree Physiology **16**:115-123

Faria T, Silvério D, Breia E, Cabral R, Abadia A, Abadia J, Pereira J, and Chaves M (1998) Differences in the response of carbon assimilation to summer stress (water deficits, high light and temperature) in four Mediterranean tree species. Physiologia Plantarum **102**:419-428

Farias-Larios J, Guzman S, and Michel A (1994) Effect of plastic mulches on the growth and yield of cucumber in a tropical region. Biological Agriculture & Horticulture **10**:303-306

Farmer D, Sivapalan M, and Jothityangkoon C (2003) Climate, soil, and vegetation controls upon the variability of water balance in temperate and semiarid landscapes: Downward approach to water balance analysis. Water Resources Research **39**

Farquhar G, Hubick K, Condon A, and Richards R (1989a) Carbon isotope fractionation and plant water-use efficiency. Pages 21-40 In: Stable isotopes in ecological research. Springer

Farquhar GD, Ehleringer JR, and Hubick KT (1989b) Carbon Isotope Discrimination and Photosyntesis. Annu. Rev. Plant Physiol. Plant Mol. Biol **40**:503-537

Farquhar GD, O'leary M, and Berry J (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Functional Plant Biology **9**:121-137

February EC, Cook GD, and Richards AE (2013a) Root dynamics influence tree–grass coexistence in an Australian savanna. Austral Ecology **38**:66-75

February EC, Higgins SI, Bond WJ, and Swemmer L (2013b) Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. Ecology **94**:1155-1164

Feder ME, Bennett AF, and Huey RB (2000) Evolutionary physiology. Annual review of ecology and systematics:315-341

Ferrez J, Davison AC, and Rebetez M (2011) Extreme temperature analysis under forest cover compared to an open field. Agricultural and Forest Meteorology **151**:992-1001

Ferrio JP, Pou A, Florez-Sarasa I, Gessler A, Kodama N, Flexas J, and Ribas-Carbó M (2012) The Péclet effect on leaf water enrichment correlates with leaf hydraulic conductance and mesophyll conductance for CO2. Plant, Cell & Environment **35**:611-625

Ferrio JP, Voltas J, and Araus JL (2003) Use of carbon isotope composition in monitoring environmental changes. Management of Environmental Quality: An International Journal **14**:82-98

Finegan B (1984) Forest Succession. Nature **312**:109-114

Fitter AH, and Hay RK. (2012) Environmental physiology of plants. Academic press,

Flanagan LB, Wever LA, and Carlson PJ (2002) Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. Global Change Biology **8**:599-615

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, and Holling CS (2004) Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. Annual Review of Ecology, Evolution, and Systematics **35**

Forbes AS, Norton DA, and Carswell FE (2014) Underplanting degraded exotic *Pinus* with indigenous conifers assists forest restoration. Ecological Management & Restoration

Fredlund MD, Wilson GW, and Fredlund DG (2002) Use of the grain-size distribution for estimation of the soil-water characteristic curve. Canadian Geotechnical Journal **39**:1103-1117

Furness NH, Jolliffe PA, and Upadhyaya MK (2005) Ultraviolet-B Radiation and Plant Competition: Experimental Approaches and Underlying Mechanisms. Photochemistry and photobiology **81**:1026-1037

Gallo J, Kuneš I, Baláš M, Nováková O, and Drury M (2014) Occurrence of frost episodes and their dynamics in height gradient above the ground in the Jizerské hory Mts. Journal of Forest Science **60**:35-41

Gebrekirstos A, Van Noordwijk M, Neufeldt H, and Mitlöhner R (2011) Relationships of stable carbon isotopes, plant water potential and growth: an approach to asses water use efficiency and growth strategies of dry land agroforestry species. Trees **25**:95-102

Gelman A, Carlin JB, Stern HS, and Rubin DB. (2014) Bayesian data analysis. Taylor & Francis,

Gênova KBD, Honda EA, and Durigan G (2007) Processos Hidrológicos em Diferentes Modelos de Plantio de Restauração de Mata Ciliar em Região de Cerrado. Rev. Inst. Flor. **19**:189-200

Genty B, Briantais J-M, and Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. BBA - General Subjects **990**:87-92

Gilks WR. (2005) Markov Chain Monte Carlo. Wiley Online Library

Givnish TJ (1999) On the Causes of Gradients in Tropical Tree Diversity. Journal of Ecology **87**:193-210

Givnish TJ (2002) Ecological constraints on the evolution of plasticity in plants. Evolutionary Ecology **16**:213-242

Godley EJ (1975) Flora and Vegetation. Pages 177-229 In: Kuschel G, (ed) Biogeography and Ecology in New Zealand. Dr. W. Junk b.v. Publishers, The Hague, Auckland, New Zealand

Golluscio R, and Oesterheld M (2007) Water use efficiency of twenty-five co-existing Patagonian species growing under different soil water availability. Oecologia **154**:207-217

Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, and Baraza E (2004) Applying Plant Facilitation to Forest Restoration: A Meta-Analysis of the Use of Shrubs as Nurse Plants. Ecological Applications **14**:1128-1138

Good AG, and Paetkau DH (1992) Identification and characterization of a hypoxically induced maize lactate dehydrogenase gene. Plant molecular biology **19**:693-697

Griffiths H (1991) Applications of Stable Isotope Technology in Physiological Ecology. Functional Ecology **5**:254-269

Griscom HP, Ashton PMS, and Berlyn GP (2005) Seedling survival and growth of native tree species in pastures: implications for dry tropical forest rehabilitation in central Panama. Forest Ecology and Management **218**:306-318

Groenendijk H. (1989) Estimation of the waterholding-capacity of soils in Europe: The compilation of a soil dataset. ISRIC

Grotkopp E, Erskine-Ogden J, and Rejmánek M (2010) Assessing potential invasiveness of woody horticultural plant species using seedling growth rate traits. Journal of Applied Ecology **47**:1320-1328

Guariguata MR, and Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. Forest Ecology and Management **148**:185-206

Gunaratne AMTA, Gunatilleke CVS, Gunatilleke IaUN, Madawala Weerasinghe HMSP, and Burslem DFRP (2011) Release from root competition promotes tree seedling survival and growth following transplantation into human-induced grasslands in Sri Lanka. Forest Ecology and Management **262**:229-236

Gunderson LH (2000) Ecological resilience--in theory and application. Annual Review of Ecology and Systematics:425-439

Halvorson JJ, Bolton H, Rossi RE, and Smith JL (1995) Evaluating shrub-associated spatial patterns of soil properties in a shrub-steppe ecosystem using multiple-variable geostatistics. Soil Science Society of America Journal **59**:1476-1487

Hammond D (1995) Post-dispersal seed and seedling mortality of tropical dry forest trees after shifting agriculture, Chiapas, Mexico. Journal of Tropical Ecology **11**:295-313

Hanba Y, Kogami H, and Terashima I (2002) The effect of growth irradiance on leaf anatomy and photosynthesis in *Acer* species differing in light demand. Plant, Cell & Environment **25**:1021-1030

Harris W (2002) Variation of inherent seed capsule splitting in populations of *Leptospermum scoparium* (Myrtaceae) in New Zealand. New Zealand Journal of Botany **40**:405-417

Havaux M (1992) Stress tolerance of photosystem II in vivo antagonistic effects of water, heat, and photoinhibition stresses. Plant Physiol **100**:424-432

Hawkins B, and Sweet G (1989) Evolutionary interpretation of a high temperature growth response in five New Zealand forest tree species. New Zealand Journal of Botany **27**:101-107

Heilmeier H, Erhard M, and Schulze E-D (1997) Biomass allocation and water use under arid conditions. Plant resource allocation:93-111

Hejcmanová P, Hejcman M, Camara AA, and Antonínová M (2009) Exclusion of livestock grazing and wood collection in dryland savannah: an effect on long-term vegetation succession. African Journal of Ecology **48**:408-417

Heneghan L, Miller SP, Baer S, Callaham MA, Montgomery J, Pavao-Zuckerman M, Rhoades CC, and Richardson S (2008) Integrating Soil Ecological Knowledge into Restoration Management. Restoration Ecology **16**:608-617

Henshaw A (2012) Factors Influencing Future Canopy Composition at Tiromoana Bush, North Canterbury, New Zealand

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, Norton D, Ojima D, Richardson DM, Sanderson EW, Valladares F, Vila M, Zamora R, and Zobel M (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography **15**:1-7

Hobbs RJ, and Cramer VA (2008) Restoration ecology: interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. Annual review of environment and resources **33**:39-61

Hobbs RJ, and Harris JA (2001) Restoration ecology: repairing the Earth's ecosystems in the new millennium. Restoration Ecology **9**:239-246

Hobbs RJ, Higgs E, and Harris JA (2009) Novel ecosystems: implications for conservation and restoration. Trends in Ecology and Evolution **24**:599-605

Hobbs RJ, and Norton DA (1996) Towards a Conceptual Framework for Restoration Ecology. Restoration Ecology **4**:93-110

Hoffmann WA, and Haridasan M (2008) The invasive grass, *Melinis minutiflora*, inhibits tree regeneration in a Neotropical savanna. Austral Ecology **33**:29-36

Holl KD, Loik ME, Lin EHV, and Samuels IA (2000) Tropical Montane Forest Restoration in Costa Rica: Overcoming Barriers to Dispersal and Establishment. Restoration Ecology **8**:339-349

Holland P, O'connor K, and Wearing A (2002) Remaking the grasslands of the open country. Pawson, e.; Brooking, T.(eds): environmental histories of New Zealand. Oxford University Press, Melbourne:69-83

Hooper E, Condit R, and Legendre P (2002) Responses of 20 Native Tree Species to Reforestation Strategies for Abandoned Farmland in Panama Ecological Applications **12**:1626-1641

Horn HS (1974) The ecology of secondary succession. Annual review of ecology and systematics:25-37

Horn R, Domżżał H, Słowińska-Jurkiewicz A, and Van Ouwerkerk C (1995) Soil compaction processes and their effects on the structure of arable soils and the environment. Soil and Tillage Research **35**:23-36

Horn R, and Smucker A (2005) Structure formation and its consequences for gas and water transport in unsaturated arable and forest soils. Soil and Tillage Research **82**:5-14

Horton P, and Ruban A (2005) Molecular design of the photosystem II light-harvesting antenna: photosynthesis and photoprotection. J Exp Bot **56**:365-373

Hu G, Liu H, Anenkhonov OA, Korolyuk AY, Sandanov DV, and Guo D (2013) Forest buffers soil temperature and postpones soil thaw as indicated by a three-year large-scale soil temperature monitoring in the forest-steppe ecotone in Inner Asia. Global and Planetary Change **104**:1-6

Inouye D (2000) The ecological and evolutionary significance of frost in the context of climate change. Ecology Letters **3**:457-463

James DG, Seymour L, Lauby G, and Buckley K (2014) Beneficial Insects Attracted to Native Flowering Buckwheats (Eriogonum Michx) in Central Washington. Environmental entomology **43**:942-948

Jeltsch F, Moloney KA, Schwager M, Körner K, and Blaum N (2011) Consequences of correlations between habitat modifications and negative impact of climate change for regional species survival. Agriculture, Ecosystems & Environment **145**:49-58

Jensen CR, Mogensen VO, Poulsen H-H, Henson IE, Aagot S, Hansen E, Ali M, and Wollenweber B (1998) Soil water matric potential rather than water content determines drought responses in field-grown lupin (*Lupinus angustifolius*). Autralian Journal of Plant Physiology **25**:253-263

Jesson L, Kelly D, and Sparrow A (2000) The importance of dispersal, disturbance, and competition for exotic plant invasions in Arthur's Pass National Park, New Zealand. New Zealand Journal of Botany **38**:451-468

Johnson C (1980) The leaf anatomy of *Leptospermum* Forst. (Myrtaceae). Australian Journal of Botany **28**:77-104

Johnson EA, and Miyanishi K (2008) Testing the assumptions of chronosequences in succession. Ecology Letters **11**:419-431

Johnson EA, and Miyanishi K. (2010) Plant disturbance ecology: the process and the response. Academic Press,

Karageorgou P, and Manetas Y (2006) The importance of being red when young: anthocyanins and the protection of young leaves of Quercus coccifera from insect herbivory and excess light. Tree Physiology **26**:613-621

Karpinski S, Wingsle G, Karpinska B, and Hallgren J (2002) Low-temperature stress and antioxidant defense mechanisms in higher plants. Oxidative stress in plants:69-103

Kass RE, and Wasserman L (1995) A reference Bayesian test for nested hypotheses and its relationship to the Schwarz criterion. Journal of the American Statistical Association **90**:928-934

Kennedy M, and Hart A (2009) Bayesian modeling of measurement errors and pesticide concentration in dietary risk assessments. Risk Analysis **29**:1427-1442

Kéry M. (2010) Introduction to WinBUGS for ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press

King WM, and Wilson JB (2006) Differentiation between native and exotic plant species in a dry grassland: realized responses to perturbation, and comparison with fundamental responses. Austral Ecology **31**:984-995

Kooten O, and Snel JF (1990) The use of chlorophyll fluorescence nomenclature in plant stress physiology. Photosynth Res **25**:147-150

Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. Oecologia **115**:445-459

Kossmann M, Sturman AP, Zawar-Reza P, Mcgowan HA, Oliphant AJ, Owens IF, and Spronken-Smith RA (2002) Analysis of the wind field and heat budget in an alpine lake basin during summertime fair weather conditions. Meteorology and Atmospheric Physics **81**:27-52

Kozlowski T (1999) Soil compaction and growth of woody plants. Scandinavian Journal of Forest Research **14**:596-619

Kozlowski TT. (2012) Flooding and plant growth. Academic Press, San Diego, California

Kozlowski TT, Kramer PJ, and Pallardy SG (1991) The Physiological Ecology of Woody Plants. Tree Physiology **8**:213-213

Kozlowski TT, and Pallardy S (1997) Physiology of wood plants. Academic Press, San Diego, California

Kozlowski TT, and Pallardy SG (2002) Acclimation and adaptive responses of woody plants to environmental stresses. Botanical Review **68**:270-334

Kramer PJSaW (1995) Soil and water. Pages 84-114 In: Kramer PJ and Boyer JS, (eds) Water Relations of Plants and Soils. Academic Press, USA

Kratsch H, and Wise R (2000) The ultrastructure of chilling stress. Plant, Cell & Environment **23**:337-350

Krause GH, and Weis E (1991) Chlorophyll Fluorescence and Photosynthesis: The Basics. Annu. Rev. Plant Physiol. Plant Mol. Biol. **42**

Kulmatiski A, and Beard KH (2013) Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. Oecologia **171**:25-37

Lambers H, Chapin FS, Iii, and Pons TL. (1998) Plant physiological ecology. Springer, New York

Lambers H, Chapin Iii FS, and Pons TL (2008) Plant water relations. Pages 163-223 In: Plant Physiological Ecology. Springer

Landis DA, Gardiner MM, and Tompkins J (2012) Using native plant species to diversify agriculture. Biodiversity and insect pests: key issues for sustainable management. Chichester: Wiley:276-292

Lawlor DW (2002) Limitation to Photosynthesis in Water-stressed Leaves: Stomata vs. Metabolism and the Role of ATP. Annals of Botany **89**:871-885

Letts MG, Johnson DRE, and Coburn CA (2010) Drought stress ecophysiology of shrub and grass functional groups on opposing slope aspects of a temperate grassland valley. Botany **88**:850-866

Lewontin RC (1969) The meaning of stability. Pages 13 Brookhaven symposia in biology

Litton CM, Sandquist DR, and Cordell S (2006) Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii. Forest Ecology and Management **231**:105-113

Litton CM, Sandquist DR, and Cordell S (2008) A non-native invasive grass increases soil carbon flux in a Hawaiian tropical dry forest. Global Change Biology **14**:726-739

Liu X, Herbert S, Hashemi A, Zhang X, and Ding G (2006) Effects of agricultural management on soil organic matter and carbon transformation-a review. Plant Soil and Environment **52**:531

Lockart N, Kavetski D, and Franks SW (2013) On the role of soil moisture in daytime evolution of temperatures. Hydrological Processes **27**:3896-3904

Lord JM (1990) The maintenance of *Poa cita* grassland by grazing. New Zealand Journal of Ecology 43-49

Lugo AE (1988) The future of the forest: ecosystem rehabilitation in the tropics. Environment: Science and Policy for Sustainable Development **30**:16-45

Lugo AE (1997) The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. Forest Ecology and Management **99**:9-19

Macfall J, Johnson G, and Kramer P (1990) Observation of a water-depletion region surrounding loblolly pine roots by magnetic resonance imaging. Proceedings of the National Academy of Sciences **87**:1203-1207

Mackay A, Mcgill C, Fountain D, and Southward R (2002) Seed dormancy and germination of a panel of New Zealand plants suitable for re-vegetation. New Zealand Journal of Botany **40**:373-382

Macmahon JA, and Holl KD (2001) A Key to Conservation Biology's Future. Conservation Biology: Research priorities for the next decade:245

Maestre FT, Bautista S, and Cortina J (2003) Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. Ecology **84**:3186-3197

Maestre FT, Bautista S, Cortina J, and Bellot J (2001) Potential for Using Facilitation by Grasses to Establish Shrubs on a Semiarid Degraded Steppe. Ecological Applications **11**:1641-1655

Maestre FT, and Cortina J (2004) Are Pinus halepensis plantations useful as a restoration tool in semiarid Mediterranean areas? Forest Ecology and Management **198**:303-317

Mannering J, Schertz D, Julian B, Logan T, Davidson J, Baker J, and Overcash M (1987) Overview of conservation tillage. Effects of conservation tillage on groundwater quality-nitrates and pesticides, 3-17

Marimon BS, and Lima EDS (2001) Caracterização fitofisionômica e levantamento florístico preliminar no pantanal dos rios Mortes-Araguaia, Cocalinho, Mato Grosso, Brasil. Acta Botanica Brasilica

Mark AF, and Mclennan B (2005) The conservation status of New Zealand's indigenous grasslands. New Zealand Journal of Botany **43**:245-270

Mark AF, Michel P, Dickinson KJ, and Mclennan B (2009) The conservation (protected area) status of New Zealand's indigenous grasslands: An update. New Zealand Journal of Botany **47**:53-60

Martin-Vertedor AI, and Dodd IC (2011) Root-to-shoot signalling when soil moisture is heterogeneous: increasing the proportion of root biomass in drying soil inhibits leaf growth and increases leaf abscisic acid concentration. Plant, Cell & Environment **34**:1164-1175

Marushia RG, and Allen EB (2011) Control of Exotic Annual Grasses to Restore Native Forbs in Abandoned Agricultural Land. Restoration Ecology **19**:45-54

Mason NW, Carswell FE, Richardson SJ, and Burrows LE (2011) Leaf palatability and decomposability increase during a 200-year-old post-cultural woody succession in New Zealand. Journal of Vegetation Science **22**:6-17

Masson ME (2011) A tutorial on a practical Bayesian alternative to null-hypothesis significance testing. Behav Res Methods **43**:679-690

Matusick G, Ruthrof KX, Brouwers NC, and Hardy GSJ (2014) Topography influences the distribution of autumn frost damage on trees in a Mediterranean-type Eucalyptus forest. Trees **28**:1449-1462

Maza-Villalobos S, Balvanera P, and Martínez-Ramos M (2011) Early Regeneration of Tropical Dry Forest from Abandoned Pastures: Contrasting Chronosequence and Dynamic Approaches. Biotropica **43**:666-675

Mcalpine KG, Timmins SM, and Westbrooke I (2009) Bone-seed (*Chrysanthemoides monilifera* ssp. *monilifera*) invasion effects on native regeneration in New Zealand coastal plant communities. New Zealand Journal of Ecology **33**:72-82

Mccarthy MA. (2007) Bayesian methods for ecology. Cambridge University Press,

Mcdonald JH. (2009) Handbook of biological statistics. Sparky House Publishing Baltimore, MD,

Mcglone M (2001) The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems. New Zealand Journal of Ecology **25**:1-15

Mcglone M (2006) Becoming New Zealanders: immigration and the formation of the biota. Pages 17-32 In: Biological Invasions in New Zealand. Springer

Mcglone MS, Duncan RP, and Heenan PB (2001) Endemism, Species Selection and the Origin and Distribution of the Vascular Plant Flora of New Zealand. Journal of Biogeography **28**:199-216

Mcgrayne SB. (2011) The theory that would not die: how Bayes' rule cracked the enigma code, hunted down Russian submarines, & emerged triumphant from two centuries of controversy. Yale University Press,

Mclaren K, and Mcdonald M (2003) The effects of moisture and shade on seed germination and seedling survival in a tropical dry forest in Jamaica. Forest Ecology and Management **183**:61-75

McQueen J, Tozer W, and Clarkson B (2006) 19 Consequences of Alien N2-Fixers on Vegetation Succession in New Zealand. Biological Invasions in New Zealand **186**:295

Mcwethy DB, Whitlock C, Wilmshurst JM, Mcglone MS, and Li X (2009) Rapid deforestation of South Island, New Zealand, by early Polynesian fires. The Holocene **19**:883-897

Measham TG (2009) Social Learning Through Evaluation: A Case Study of Overcoming Constraints for Management of Dryland Salinity. Environmental Management **43**:1096-1107

Melander B, and Jørgensen MH (2005) Soil steaming to reduce intrarow weed seedling emergence. Weed Research **45**:202-211

Mengistu T, Teketay D, Hulten H, and Yemshaw Y (2005) The role of enclosures in the recovery of woody vegetation in degraded dryland hillsides of central and northern Ethiopia. Journal of Arid Environments **60**:259-281

Meurk CD, Norton DA, and Lord JM (1989) The effect of grazing and its removal from grassland reserves in Canterbury. Management of New Zealand's Natural Estate:72-75

Meziane D, and Shipley B (2001) Direct and indirect relationships between specific leaf area, leaf nitrogen and leaf gas exchange. Effects of irradiance and nutrient supply. Annals of Botany **88**:915-927

Montalvo AM, Mcmillan PA, and Allen EB (2002) The relative importance of seeding method, soil ripping, and soil variables on seeding success. Restoration Ecology **10**:52-67

Moreno-Gutiérrez C, Dawson TE, Nicolás E, and Querejeta JI (2012) Isotopes reveal contrasting water use strategies among coexisting plant species in a Mediterranean ecosystem. New Phytologist **196**:489-496

Morison J (1996) General Plant Ecophysiology. J Exp Bot:37-48

Moro M, Pugnaire F, Haase P, and Puigdefábregas J (1997) Effect of the canopy of *Retama sphaerocarpa* on its understorey in a semiarid environment. Functional Ecology **11**:425-431

Morris W. (1969) American heritage dictionary of the English language. American heritage,

Mueller EN, Wainwright J, Parsons AJ, and Turnbull L (2014) Land Degradation in Drylands: An Ecogeomorphological Approach. Pages 1-9 In: Patterns of Land Degradation in Drylands. Springer

Mullineaux LS, Peterson CH, Micheli F, and Mills SW (2003) Successional Mechanism Varies along a Gradient in Hydrothermal Fluid Flux at Deep-Sea Vents. Ecological Monographs **73**:523-542

Nawaz MF, Bourrie G, and Trolard F (2013) Soil compaction impact and modelling. A review. Agronomy for sustainable development **33**:291-309

Nelms KD, Ballinger B, and Boyles A (2007) Wetland management for waterfowl handbook. Mississippi River Trust. Natural Resources Conservation Service, Mississippi, USA

Nelson JA, Gotwalt PS, and Snodgrass JW (2003) Swimming performance of blacknose dace (*Rhinichthys atratulus*) mirrors home-stream current velocity. Canadian Journal of Fisheries and Aquatic Sciences **60**:301-308

Nepstad D, Lefebvre P, Lopes Da Silva U, Tomasella J, Schlesinger P, Solorzano L, Moutinho P, Ray D, and Guerreira Benito J (2004) Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. Global Change Biology **10**:704-717

Nicholls N (2004) The Changing Nature of Australian Droughts. Climatic Change **63**:323-336

Nilsen ET, and Orcutt DM (1996) Physiology of plants under stress. Abiotic factors. Physiology of plants under stress. Abiotic factors.

Niyogi KK (1999) Photoprotection revisited: genetic and molecular approaches. Annu Rev Plant Biol **50**:333-359

Norton BDA, and Miller CJ (2000) Some issues and options for the conservation of native biodiversity in rural New Zealand. Ecological Management & Restoration **1**:26-34

Norton D. (2006) Glenmore Station Environmental Report. University of Canterbury, Christhurch

Norton DA. (2012) Tiromoana Bush Restoration Management Plan July 2012 – June 2017, Canterbury, New Zealand

Norton DA, and Reid N. (2013) Nature and farming: sustaining native biodiversity in agricultural landscapes. CSIRO Pub, Collingwood, Vic

O'Brien G, O'Keefe P, Rose J, and Wisner B (2006) Climate change and disaster management. Disasters **30**:64-80

Odum EP (1985) Trends expected in stressed ecosystems. BioScience **35**:419-422

Ort DR (2001) When There Is Too Much Light. Plant Physiol **125**:29-32

Ort DR, Oxborough K, and Wise RR (1994) Depressions of photosynthesis in crops with water deficits. Photoinhibition of Photosynthesis from Molecular Mechanisms to the Field:315-329

Özgöz E (2009) Long term conventional tillage effect on spatial variability of some soil physical properties. Journal of Sustainable Agriculture **33**:142-160

Pacala SW, Canham CD, Saponara J, Jr. JaS, Kobe RK, and Ribbens E (1996) Forest Models Defined by Field Measurements: Estimation, Error Analysis and Dynamics. Ecological Monographs **66**:1-43

Padilla FM, Miranda JD, Jorquera MJ, and Pugnaire FI (2009) Variability in amount and frequency of water supply affects roots but not growth of arid shrubs. Plant Ecology **204**:261-270

Padilla FM, and Pugnaire FI (2009) Species Identity and Water Availability Determine Establishment Success Under the Canopy of *Retama sphaerocarpa* Shrubs in a Dry Environment. Restoration Ecology **17**:900-907

Page K, Dang Y, and Dalal R (2013) Impacts of conservation tillage on soil quality, including soil-borne crop diseases, with a focus on semi-arid grain cropping systems. Australasian Plant Pathology **42**:363-377

Pallardy SG (2008) Chapter 3 - Vegetative Growth. Pages 39-86 In: Pallardy SG, (ed) Physiology of Woody Plants (Third Edition). Academic Press, San Diego

Parrotta JA (1999) Productivity, nutrient cycling, and succession in single-and mixed-species plantations of *Casuarina equisetifolia, Eucalyptus robust*a, and *Leucaena leucocephala* in Puerto Rico. Forest Ecology and Management **124**:45-77

Parrotta JA, Turnbull JW, and Jones N (1997) Catalyzing native forest regeneration on degraded tropical lands. Forest Ecology and Management **99**:1-7

Passioura J (1991) Soil structure and plant growth. Soil Research **29**:717-728

Pavliscak LL, Fehmi JS, and Smith SE (2015) Assessing Emergence of a Long-Lived Monocarpic Succulent in Disturbed, Arid Environments: Evaluating Abiotic Factors in Effective Agave Restoration by Seed. Arid Land Research and Management **29**:98-109

Payne T, and Norton DA (2011) Influence of shade on soil and foliage water in a depleted short tussock grassland, Mackenzie Basin. New Zealand Natural Sciences **36**:21-31

Pearcy RW, Ehleringer JR, Mooney HA, and Rundel PW. (1989) Plant physiological ecology: field methods and instrumentation. Chapman and Hall Ltd,

Peltzer DA, and Köchy M (2001) Competitive effects of grasses and woody plants in mixed-grass prairie. Journal of Ecology **89**:519-527

Pfeifer J, Faget M, Walter A, Blossfeld S, Fiorani F, Schurr U, and Nagel KA (2014) Spring barley shows dynamic compensatory root and shoot growth responses when exposed to localised soil compaction and fertilisation. Functional Plant Biology **41**:581

Polis GA, Sears AL, Huxel GR, Strong DR, and Maron J (2000) When is a trophic cascade a trophic cascade? Trends Ecol Evol **15**:473-475

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, and Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytologist **193**:30-50

Poorter L (1999) Growth Responses of 15 Rain-Forest Tree Species to a Light Gradient: The Relative Importance of Morphological and Physiological Traits. Functional Ecology **13**:396-410

Poorter L (2005) Resource capture and use by tropical forest tree seedlings and their consequences for competition. Biotic interactions in the tropics: Their role in the maintenance of species diversity:35-64

Proffitt A, Bendotti S, Howell M, and Eastham J (1993) The effect of sheep trampling and grazing on soil physical properties and pasture growth for a red-brown earth. Crop and Pasture Science **44**:317-331

Pugnaire FI, Haase P, and Puigdefábregas J (1996) Facilitation between Higher Plant Species in a Semiarid Environment. Ecology **77**:1420-1426

Pyke DA, and Knick ST (2005) Plant invaders, global change and landscape restoration. African Journal of Range & Forage Science **22**:75-83

Queiroz C, Beilin R, Folke C, and Lindborg R (2014) Farmland abandonment: threat or opportunity for biodiversity conservation? A global review. Front Ecol Environ **12**:288-296

Raftery AE (1995) Bayesian model selection in social research. Sociological methodology **25**:111-164

Reay SD, and Norton DA (1999) *Phormium tenax*, an unusual nurse plant. New Zealand Journal of Ecology **23**:81-85

Redding T, Winkler R, Teti P, Spittlehouse D, Boon S, Rex J, Dubé S, Moore R, Wei A, and Carver M (2008) Mountain pine beetle: From lessons learned to community-based solutions Journal of Ecosystems and Management **9**:33-50

Reddy AR, Chaitanya KV, and Vivekanandan M (2004) Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. Journal of plant physiology **161**:1189-1202

Rees M, Condit R, Crawley M, Pacala S, and Tilman D (2001) Long-term studies of vegetation dynamics. Science **293**:650-655

Rendig VV, and Taylor HM. (1989) Principles of soil-plant interrelationships. McGraw-Hill Publishing Company,

Research DOSaI, Development MOWA, Federation NZC, Association NZC, and Zealand NZGSTLRCON (1986) New Zealand Standard Pages 7 Methods of Testing Soils for Civil Engineering Purposes Standards New Zealand, New Zealand

Ricklefs RE, and Wikelsk M (2002) The physiology/life-history nexus. Trends in Ecology and Evolution **17**:462-468

Riginos C (2009) Grass competition suppresses savanna tree growth across multiple demographic stages. Ecology **90**:335-340

Rogers GM, Walker S, and Lee WG. (2005) The role of disturbance in dryland New Zealand: past and present. Department of Conservation, Wellington

Romic D, Borosic J, Poljak M, and Romic M (2003) Polyethylene mulches and drip irrigation increase growth and yield in watermelon (*Citrullus lanatus* L.). European journal of horticultural science **68**:192-198

Romic D, Ondrasek G, Romic M, Josip B, Vranjes M, and Petosic D (2008) Salinity and irrigation method affect crop yield and soil quality in watermelon (*Citrullus lanatus* L.) growing. Irrigation and Drainage **57**:463-469

Ronghua Y, Mark AF, and Wilson JB (1984) Aspects of the ecology of the indigenous shrub *Leptospermum scoparium* (Myrtaceae) in New Zealand. New Zealand Journal of Botany **22**:483-507

Rose A, Basher L, Wiser S, Platt K, and Lynn I (1998) Factors predisposing short-tussock grasslands to *Hieracium* invasion in Marlborough, New Zealand. New Zealand Journal of Ecology **22**:121-140

Rose AB, and Frampton CM (1999) Effects of microsite characteristics on *Hieracium* seedling establishment in tall-and short-tussock grasslands, Marlborough, New Zealand. New Zealand Journal of Botany **37**:107-118

Rose AB, and Frampton CM (2007) Rapid short-tussock grassland decline with and without grazing, Marlborough, New Zealand. New Zealand Journal of Ecology **31**:232-244

Rose AB, Suisted PA, and Frampton CM (2004) Recovery, invasion, and decline over 37 years in a Marlborough short-tussock grassland, New Zealand. New Zealand Journal of Botany **42**:77-87

Rossiter NA, Setterfield SA, Douglas MM, and Hutley LB (2003) Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. Diversity and Distributions **9**:169-176

Roundy BA, Heydari H, Watson C, Smith SE, Munda B, and Pater M (2001) Summer Establishment of Sonoran Desert Species for Revegetation of Abandoned Farmland Using Line Source Sprinkler Irrigation. Arid Land Research and Management **15**:23-39

Rovai AS, Soriano-Sierra EJ, Pagliosa PR, Cintrón G, Schaeffer-Novelli Y, Menghini RP, Coelho-Jr C, Horta PA, Lewis Iii RR, and Simonassi JC (2012) Secondary succession impairment in restored mangroves. Wetlands ecology and management **20**:447-459

Roy B, and New Zealand Plant Protection S. (2004) An illustrated guide to common weeds of New Zealand. New Zealand Plant Protection Society, Lincoln, N.Z

Royer PD, Cobb NS, Clifford MJ, Huang CY, Breshears DD, Adams HD, and Villegas JC (2011) Extreme climatic event-triggered overstorey vegetation loss increases understorey solar input regionally: primary and secondary ecological implications. Journal of Ecology **99**:714-723

Ruiz-Jaen MC, and Aide TM (2005) Restoration Success: How Is It Being Measured? Restoration Ecology **13**:569-577

Ryan K, and Hunt J (2005) The effects of UVB radiation on temperate southern hemisphere forests. Environmental Pollution **137**:415-427

Sánchez JF, and Quiles MJ (2006) Studying photosynthesis by measuring fluorescence. JBE **41**:34-37

Saunders A, and Norton DA (2001) Ecological restoration at Mainland Islands in New Zealand. Biological Conservation **99**:109-119

Saxton K, and Rawls W (2006) Soil water characteristic estimates by texture and organic matter for hydrologic solutions. Soil Science Society of America Journal **70**:1569-1578

Scartazza A, Vaccari FP, Bertolini T, Di Tommasi P, Lauteri M, Miglietta F, and Brugnoli E (2014) Comparing integrated stable isotope and eddy covariance estimates of water-use efficiency on a Mediterranean successional sequence. Oecologia **176**:581-594

Schleuning M, Niggemann M, Becker U, and Matthies D (2009) Negative effects of habitat degradation and fragmentation on the declining grassland plant Trifolium montanum. Basic and Applied Ecology **10**:61-69

Schlüter U, and Crawford RM (2001) Long-term anoxia tolerance in leaves of *Acorus calamus* L. and *Iris pseudacorus* L. J Exp Bot **52**:2213-2225

Schönberger I (2002) Biosystematics and taxonomy of the *Ozothamnus leptophyllus* (Compositae) complex in New Zealand. Doctorate. University of Canterbury. Botany

Scott NA, Saggar S, and Mcintosh PD (2001) Biogeochemical impact of *Hieracium* invasion in New Zealand's grazed tussock grasslands: sustainability implications. Ecological Applications **11**:1311-1322

Seastedt TR, Hobbs RJ, and Suding KN (2008) Management of novel ecosystems: are novel approaches required? Frontiers in Ecology and the Environment **6**:547-553

Shackelford N, Hobbs RJ, Heller NE, Hallett LM, and Seastedt TR (2013) Finding a middle-ground: the native/non-native debate. Biological Conservation **158**:55-62

Sorte CJ, Ibanez I, Blumenthal DM, Molinari NA, Miller LP, Grosholz ED, Diez JM, D'Antonio CM, Olden JD, Jones SJ, and Dukes JS (2013) Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecol Lett **16**:261-270

Sperry JS, and Hacke UG (2002) Desert Shrub Water Relations with Respect to Soil Characteristics and Plant Functional Type. Functional Ecology **16**:367-378

Spicer J, and Gaston K. (2009) Physiological diversity: Ecological implications. John Wiley & Sons,

Standish RJ, Cramer VA, Wild SL, and Hobbs RJ (2007) Seed dispersal and recruitment limitation are barriers to native recolonization of old-fields in western Australia. Journal of Applied Ecology **44**:435-445

Standish RJ, Sparrow AD, Williams PA, and Hobbs RJ (2009) A State-and-Transition Model for the Recovery of Abandoned Farmland in New Zealand. Pages 1889-1205 In: Hobbs RJ and Suding KN, (eds) New Models for Ecosystem Dynamics and Restoration. Island Press, USA

Stephens JMC, Molan PC, and Clarkson BD (2005) A review of *Leptospermum scoparium* (Myrtaceae) in New Zealand. New Zealand Journal of Botany **43**:431-449

Stevenson BA, and Smale MC (2005) Seed bed treatment effects on vegetation and seedling establishment in a New Zealand pasture one year after seeding with native woody species. Ecological Management and Restoration **6**:124-131

Suding KN, and Hobbs RJ (2009) Models of Ecosystem Dynamics as Frameworks for Restoration Ecology. Pages 3-21 In: Hobbs RJ and Suding KN, (eds) New Models for Ecosystem Dynamics and Restoration. Island Press, USA

Sullivan JJ, Williams PJ, and Timmins SM (2007) Secondary forest succession differs through naturalised gorse and native kānuka near Wellington and Nelson. New Zealand Journal of Ecology **31**:22-38

Sweeney BW, Czapka SJ, and Yerkes T (2002) Riparian Forest Restorration: Increasing Success by Reducing Plant Competition and Herbivory. Restoration Ecology **10**:392-400

Syrett P, Forrester GJ, Harman HM, Meurk CD, Partridge TR, and Smith LA (2012) Predicting possible negative impacts of weed biocontrol by artificially suppressing invasive hawkweed in New Zealand's tussock grasslands. BioControl **57**:117-129

Taiz L, and Zeiger E. (2010) Plant physiology. Sinauer Associates, Sunderland, MA

Tang X, Liu S, Liu J, and Zhou G (2009) Effects of vegetation restoration and slope positions on soil aggregation and soil carbon accumulation on heavily eroded tropical land of Southern China. Journal of Soils and Sediments **10**:505-513

Terwilliger V, Kitajima K, Roux-Swarthout L, Mulkey S, and Wright S (2001) Intrinsic water-use efficiency and heterotrophic investment in tropical leaf growth of two Neotropical pioneer tree species as estimated from δ13C values. New Phytologist **152**:267-281

Tezara W, Urich R, Coronel I, Marín O, and Herrera A (2010) Asimilación de carbono, eficiencia de uso de agua y actividad fotoquímica en xerófitas de ecosistemas semiáridos de Venezuela. Ecosistemas **19**:67-78

Thaxton JM, Cole TC, Cordell S, Cabin RJ, Sandquist DR, and Litton CM (2010) Native Species Regeneration Following Ungulate Exclusion and Nonnative Grass Removal in a Remnant Hawaiian Dry Forest1. Pacific Science **64**:533-544

Tognetti R, Minnocci A, Peñuelas J, Raschi A, and Jones MB (2000) Comparative field water relations of three Mediterranean shrub species co-occurring at a natural CO2 vent. J Exp Bot **51**:1135-1146

Tompkins J-M (2010) Ecosystem services provided by native New Zealand plants in vineyards. Lincoln University

Towns DR, Simberloff D, and Atkinson IA (1997) Restoration of New Zealand islands: redressing the effects of introduced species. Pacific Conservation Biology **3**:99-124

Travis J, Mcmanu MG, and Baer CF (1999) Sources of variation in physiological phenotypes and their evolutionary significance. American Zoologist **39**:422-433

Treca B, and Tamba S (1997) Role of birds on the regeneration of the woody *Boscia senegalensis* (Pers.) Lam. in Sahelian savanna in North Senegal. Revue d'Ecologie (France)

Trotter C, Tate K, Scott N, Townsend J, Wilde H, Lambie S, Marden M, and Pinkney T (2005) Afforestation/reforestation of New Zealand marginal pasture lands by indigenous shrublands: the potential for Kyoto forest sinks. Annals of Forest Science **62**:865-871

Tyree MT (2003) Desiccation Tolerance of Five Tropical Seedlings in Panama. Relationship to a Field Assessment of Drought Performance. Plant Physiol **132**:1439-1447

Vallejo R, Aronson J, Pausas JG, and Cortina J (2006) Restoration of Mediterranean woodlands. Restoration ecology: The new frontier:193-207

Van Den Driessche R (1992) Absolute and relative growth of Douglas-fir seedlings of different sizes. Tree Physiology **10**:141-152

Van Langevelde F, Van De Vijver CA, Kumar L, Van De Koppel J, De Ridder N, Van Andel J, Skidmore AK, Hearne JW, Stroosnijder L, and Bond WJ (2003) Effects of fire and herbivory on the stability of savanna ecosystems. Ecology **84**:337-350

Vartapetian BB, and Jackson MB (1997) Plant Adaptations to Anaerobic Stress. Ann Bot **79**:3-20

Veenendaal E, Swaine M, Agyeman V, Blay D, Abebrese I, and Mullins C (1996) Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. Journal of Ecology:83-90

Vitousek PM, D'antonio CM, Loope LL, Rejmánek M, and Westbrooks R (1997) Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology **21**:1-16

Vogel J, Ehleringer J, Hall A, and Farquhar G (1993) Variability of carbon isotope fractionation during photosynthesis. Pages 29-46 Stable isotopes and plant carbon-water relations. Academic Press Inc.

Vosper S, and Brown A (2008) Numerical simulations of sheltering in valleys: the formation of nighttime cold-air pools. Boundary-layer meteorology **127**:429-448

Walker B (1987) A general model of savanna structure and function. IUBS MONOGR. SER. 1987.

Walker S (2000) Post-pastoral changes in composition and guilds in a semi-arid conservation area, Central Otago, New Zealand. New Zealand Journal of Ecology **24**:123-137

Walker S, Cieraad E, Monks A, Burrows L, Wood J, Price R, Rogers G, and Lee B (2009a) Long-term dynamics and rehabilitation of Woody Ecosystems in Dryland South Island, New Zealand. Pages 99-111 In: Hobbs RJ and Suding KN, (eds) New Models for Ecosystem Dynamics and Restoration. Island Press, USA

Walker S, King N, Monks A, Williams S, Burrows L, Cieraad E, Meurk C, Overton JM, Price R, and Smale M (2009b) Secondary woody vegetation patterns in New Zealand's South Island dryland zone. New Zealand Journal of Botany **47**:367-393

Walker S, Lee WG, and Rogers GM (2003a) The woody vegetation of Central Otago, New Zealand: its present and past distribution and future restoration needs. Science for Conservation **226**:4.1

Walker S, Lee WG, and Rogers GM (2004) The woody vegetation of Central Otago, New Zealand. New Zealand Journal of Botany **42**:589-612

Walker S, Wilson DJ, Norbury G, Monks A, and Tanentzap AJ (2014) Complementarity of indigenous flora in shrublands and grasslands in a New Zealand dryland landscape. New Zealand Journal of Ecology **38**:230-241

Walker S, Wilson JB, and Lee WG (2003b) Recovery of short tussock and woody species guilds in ungrazed *Festuca novae-zelandiae* short tussock grassland with fertiliser or irrigation. New Zealand Journal of Ecology **27**:179-189

Walker S, Wilson JB, and Lee WG (2005) Does fluctuating resource availability increase invasibility? Evidence from field experiments in New Zealand short tussock grassland. Biological Invasions **7**:195-211

Wardle DA, Barker GM, Yeates GW, Bonner KI, and Ghani A (2001) Introduced Browsing Mammals in New Zealand Natural Forests: Aboveground and Belowground Consequences. Ecological Monographs **71**:587-614

Wardle P. (2002) Vegetation of New Zealand. Blackburn Press, Caldwell, N.J

Wardle P, Mark A, and Baylis G (1973) Vegetation and landscape of the West Cape District, Fiordland, New Zealand. New Zealand journal of botany **11**:599-626

Watkinson AR, and Powell JC (1997) The Life History and Population Structure of *Cycas armstrongii* in Monsoonal Northern Australia. Oecologia **111**:341-349

Webb RS, Rosenzweig CE, and Levine ER (1993a) Specifying land surface characteristics in general circulation models: Soil profile data set and derived water-holding capacities. Global Biogeochemical Cycles **7**:97

Webb RS, Rosenzweig CE, and Levine ER (1993b) Specifying land surface characteristics in general circulation models: Soil profile data set and derived water-holding capacities. Global Biogeochemical Cycles **7**:97-108

Westoby M, Falster DS, Moles AT, Vesk PA, and Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology and Systematics:125-159

Whitford WG. (2002) Ecology of desert systems. Academic Press,

Widmann P, Martin K, and Langenberger G (2005a) Seed dispersal and predation across a grassland-forest ecotone in southern Palawan, Philippines

Widmann P, Martin K, and Langenberger G (2005b) Seed dispersal and predation across a grassland-forest ecotone in southern Palawan, Philippines. Conference on International Agricultural Research for Development, Stuttgart-Hohenheim, Germany2005b, [insert place of publication]

Williams PA, and Karl BJ (2002) Birds and small mammals in kanuka (*Kunzea ericoides*) and gorse (*Ulex europaeus*) scrub and the resulting seed rain and seedling dynamics. New Zealand Journal of Ecology **26**:31-42

Wilmshurst JM, Mcglone MS, Leathwick JR, and Newnham RM (2007) A pre-deforestation pollen-climate calibration model for New Zealand and quantitative temperature reconstructions for the past 18 000 years BP. Journal of Quaternary Science **22**:535-547

Wilson DJ, Lee WG, Webster RA, and Allen RB (2003) Effects of possums and rats on seedling establishment at two forest sites in New Zealand. New Zealand Journal of Ecology **27**:147-155

Wilson J (1996) Shade-stimulated growth and nitrogen uptake by pasture grasses in a subtropical environment. Crop and Pasture Science **47**:1075-1093

Winkel VK, Roundy BA, and Cox JR (1991) Influence of seedbed microsite characteristics on grass seedling emergence. Journal of Range Management:210-214

Worthy TH, and Holdaway RN. (2002) The lost world of the moa: prehistoric life of New Zealand. Indiana University Press,

Wright DM, Tanentzap AJ, Flores O, Husheer SW, Duncan RP, Wiser SK, and Coomes DA (2012) Impacts of culling and exclusion of browsers on vegetation recovery across New Zealand forests. Biological Conservation **153**:64-71

Wright I, and Westoby M (2000) Cross-species relationships between seedling relative growth rate, nitrogen productivity and root vs leaf function in 28 Australian woody species. Functional Ecology **14**:97-107

Yang Y, Yao Y, Xu G, and Li C (2005) Growth and physiological responses to drought and elevated ultraviolet-B in two contrasting populations ofHippophae rhamnoides. Physiologia Plantarum **124**:431-440

Yates CJ, Norton DA, and Hobbs RJ (2000) Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: implications for restoration. Austral Ecology **25**:36-47

Yuan W, Luo Y, Richardson AD, Oren R, Luyssaert S, Janssens IA, Ceulemans R, Zhou X, Grünwald T, and Aubinet M (2009) Latitudinal patterns of magnitude and interannual variability in net ecosystem exchange regulated by biological and environmental variables. Global Change Biology **15**:2905-2920

Zhang L, Dawes W, and Walker G (2001) Response of mean annual evapotranspiration to vegetation changes at catchment scale. Water Resources Research **37**:701-708

Zhao WZ, Xiao HL, Liu ZM, and Li J (2005) Soil degradation and restoration as affected by land use change in the semiarid Bashang area, northern China. Catena **59**:173-186

Zhou S, Medlyn B, Sabaté S, Sperlich D, and Prentice IC (2014) Short-term water stress impacts on stomatal, mesophyll and biochemical limitations to photosynthesis differ consistently among tree species from contrasting climates. Tree Physiology **34**:1035-1046

8. Appendix

8.1 Statistical Models

8.1.1 Probability of Survival

```
model;
{
for(i in 1:n) {# n = number of plants of one species (including replicates)
Y[i]~dbern(s[i])# Bernoulli distribution
}
# mixed model
# logit link
for(i in 1:n) {
s[i]<- 1/(1+exp(-phi[i]))
}
# regression
for(i in 1:n) {
phi[i] <- beta[trt[i]]+epsilon[plot[i]]
}
# priors
for(j in 1:t){# t = number of treatments (7 = Rank Grass Sites; 4 = Degraded Short-Tussock sites
beta[j] ~ dnorm(0,1.0E-5)
}
for(k in 1:k){# k = number of plots
epsilon[k] ~ dnorm(0,tau)
}
tau ~ dgamma(.01,.01)
# monitors
for(j in 1:t){
s.est[j] <-1/(1+exp(-beta[j]))
}
# to do  a Tukey test
```

```
for(j1 in 1:t){ # treatment 1 to t
for(j2 in 1:t){ # treatment 1 to t
S[j1,j2] <- step(beta[j1]-beta[j2])
}}
}
# INITS
list(tau=1, beta=c(0,0,0,0))# depends on the number of treatment used in the trial, either 4 (Degraded Short-tussock sites) or 7 (Rank Grass sites)
```

8.1.2 Relative Height Increment

```
model;
{
for(i in 1:n) {n = number of plants in total, including replicates
# the observed RHI has a normal distribution (between 0 and 1)
# parameters of normal distribution depend on treatment
RHI[i]~dnorm(mu[i],tau.RHI)
}
# priors
for (j in 1:t){t = number of treatments
beta[j] ~ dnorm(0,1.0E-5)
}
for (k in 1:k){ k = number of plots
epsilon[k] ~ dnorm(0,tau.RHI)
}
tau.RHI ~ dgamma(0.1,0.1)
# monitors: expected RHI for each treatment
for(i in 1:n){
mu[i] <- beta[trt[i]]+epsilon[plot[i]]
}
# post-hoc test to compare treatments
```

```
for(j1 in 1:t){ # treatment 1 to t
for(j2 in 1:t){ # treatment 1 to t
RHItuk[j1,j2] <- step(beta[j1]-beta[j2])
}}
}
# INITS
list(beta=c(0,0,0,0))# according to number of treatments, either 4 (Degraded Short-tussock sites)
or 7 (Rank Grass sites)
```

8.1.3 Soil Water Content

```
model;
{
for(i in 1:n) {n = number of soil samples
# the observed water content has beta distribution (between 0 and 1)
# parameters of beta distribution depend on treatment
Y[i]~dbeta(a[trt[i]],b[trt[i]])
}
# priors
for(j in 1:t){t = number of treatments
a[j] ~ dgamma(0.1,0.1)
b[j] ~ dgamma(0.1,0.1)
}
# monitors: expected water moisture for each treatment
for(j in 1:t){
SW.est[j] <-a[j]/(b[j]+a[j])
}
# post-hoc test to compare expected soil water content between treatments
for(j1 in 1:t){ # treatment 1 to t
for(j2 in 1:t){ # treatment 1 to t
SWtuk[j1,j2] <- step(SW.est[j1]-SW.est[j2])
}}
```

```
}
# INITS
list(a=c(1,1,1,1),b=c(1,1,1,1))# ranged from 4 to 7 according to the number of treatments used in the trial
```

8.1.4 Chlorophyll Fluorescence

```
model;
{
for(i in 1:n) {n = number of plants
# the observed Fluorescence has a normal distribution
# parameters of normal distribution depend on treatment
Y[i]~dnorm(mu[i],tau.Y)
}
# priors
for (j in 1:t){t =  number of treatments
beta[j] ~ dnorm(0,1.0E-5)
}
for (k in 1:k){k = number of plots
epsilon[k] ~ dnorm(0,tau.Y)
}
tau.Flu ~ dgamma(0.1,0.1)
# monitors: expected Fluorescence for each treatment
for(i in 1:n){
mu[i] <- beta[trt[i]]+epsilon[plot[i]]
}
# post-hoc test to compare expected Y-values between treatments
for(j1 in 1:7){ # treatment 1 to 7
for(j2 in 1:7){ # treatment 1 to 7
Flu.tuk[j1,j2] <- step(beta[j1]-beta[j2])
}}
}
```

```
# INITS
list(beta=c(0,0,0,0,0,0,0))#seven treatments implemented in the Rank Grass sites
```

8.1.5 Carbon Isotope Analysis

```
model;
{
for(i in 1:n) {n = number of samples
# the calculated 13C has a normal distribution
# parameters of normal distribution depend on treatment
Y[i]~dnorm(mu[i],tau.C)
}
# priors
for (j in 1:t){t = number of treatments
beta[j] ~ dnorm(0,1.0E-5)
}
for (k in 1:k){k = number of plots
epsilon[k] ~ dnorm(0,tau.C)
}
tau.C ~ dgamma(0.1,0.1)
# monitors: expected 13C for each treatment
for(i in 1:n{
mu[i] <- beta[trt[i]]+epsilon[sample[i]]
}
# post-hoc test to compare expected 13C between treatments
for(j1 in 1:t){ # treatment 1 to t
for(j2 in 1:t){ # treatment 1 to t
C.tuk[j1,j2] <- step(beta[j1]-beta[j2])
}}
}
# INITS
list(beta=c(0,0,0,0))# according to the number of treatments in each trial, either 4 or 7.
```

8.2 Soil Analyses

8.2.1 Soil Physical Analyses – Soil Classification

- *Particle size distribution: Dry Sieving and Sedimentation tests*

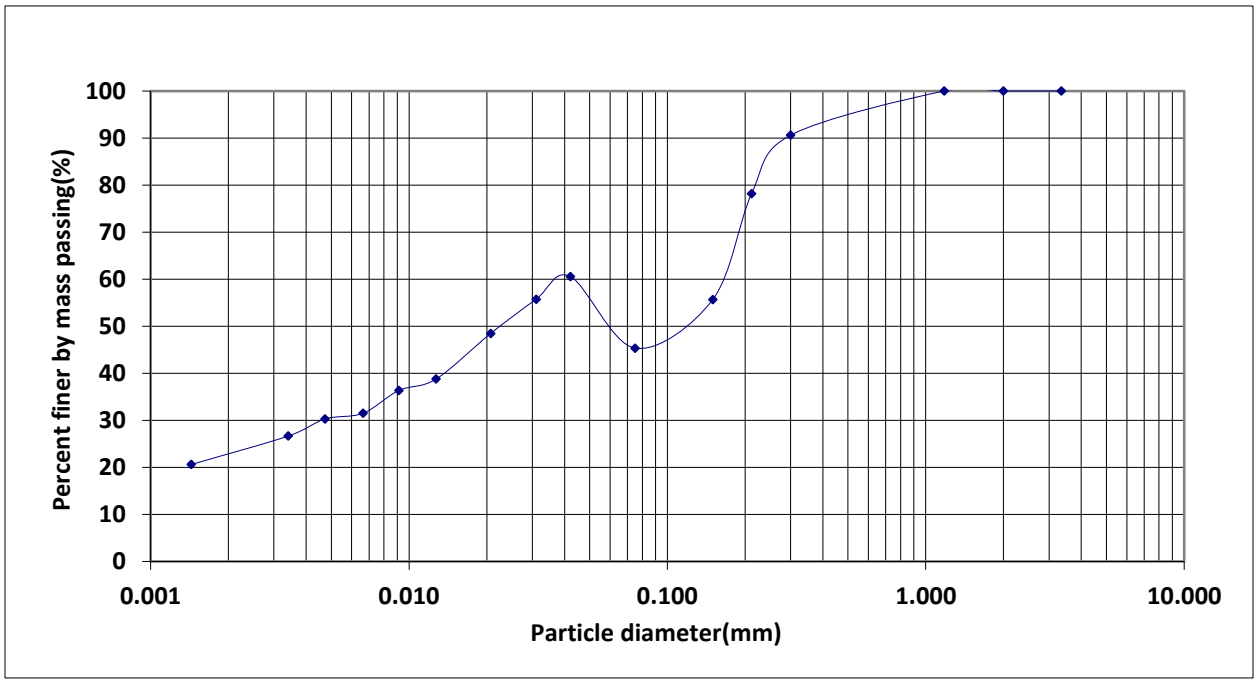


Figure 8-1 Particle size distribution curve – Tiromoana Bush.

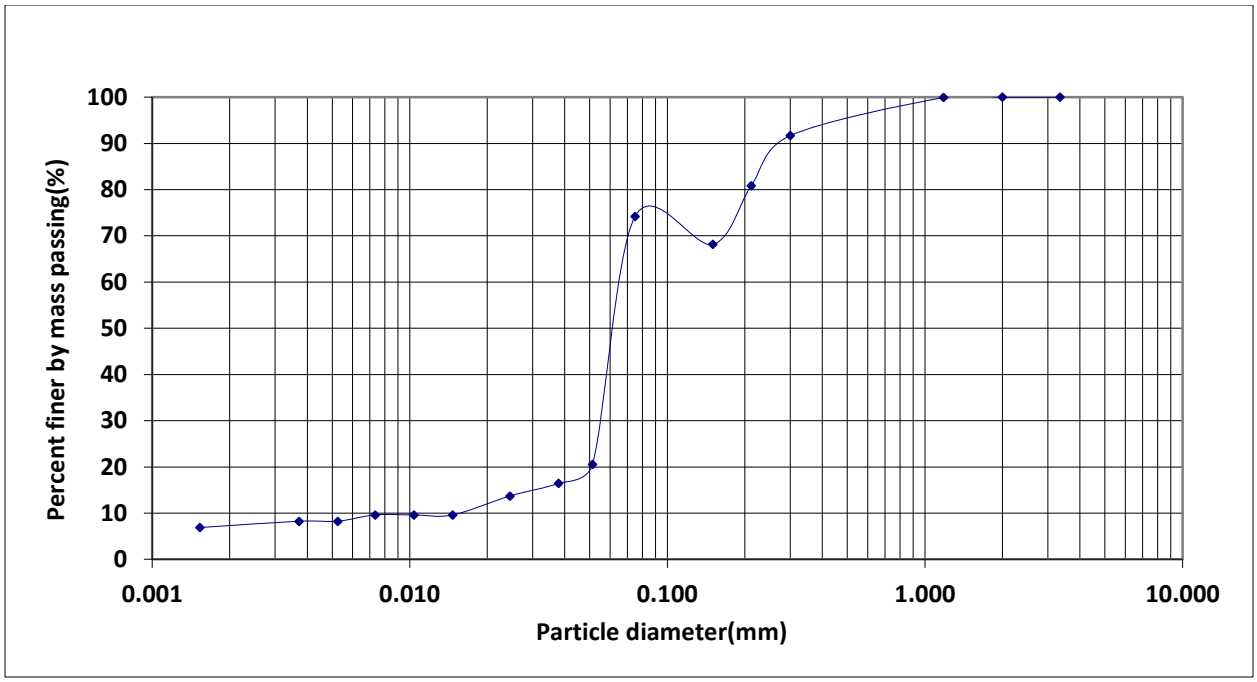


Figure 8-2 Particle size distribution curve – The Willows Reserve.

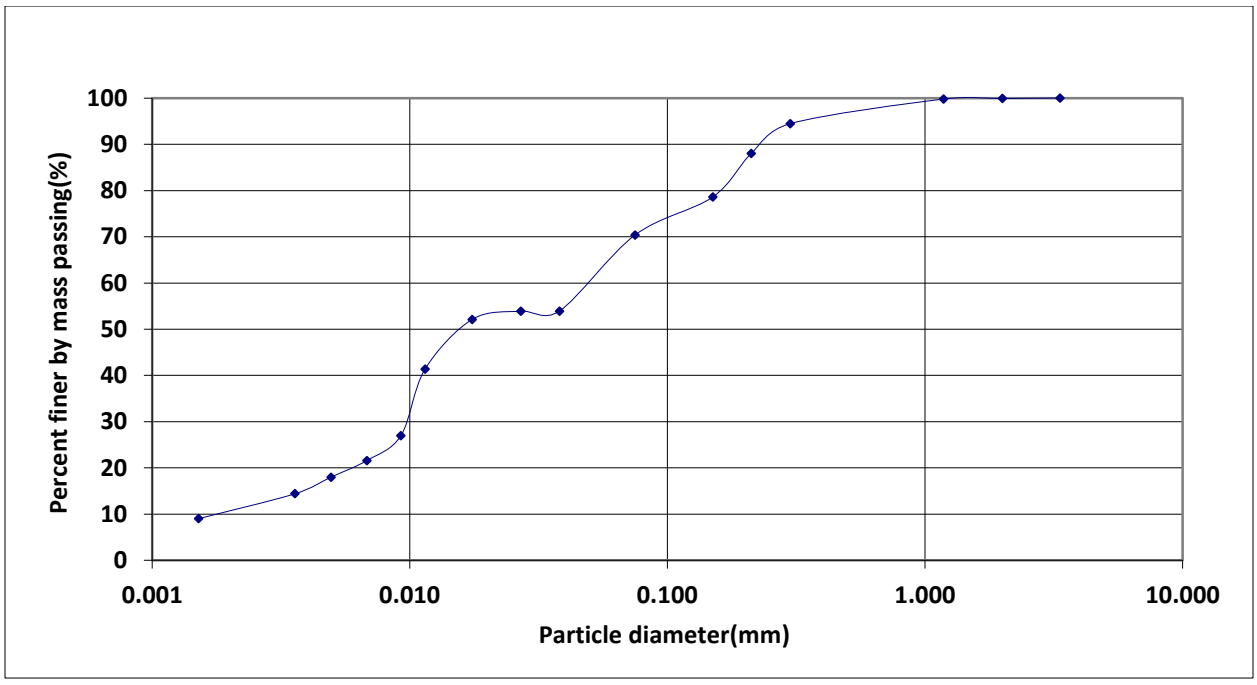


Figure 8-3 Particle size distribution curve – Dierickx Farm.

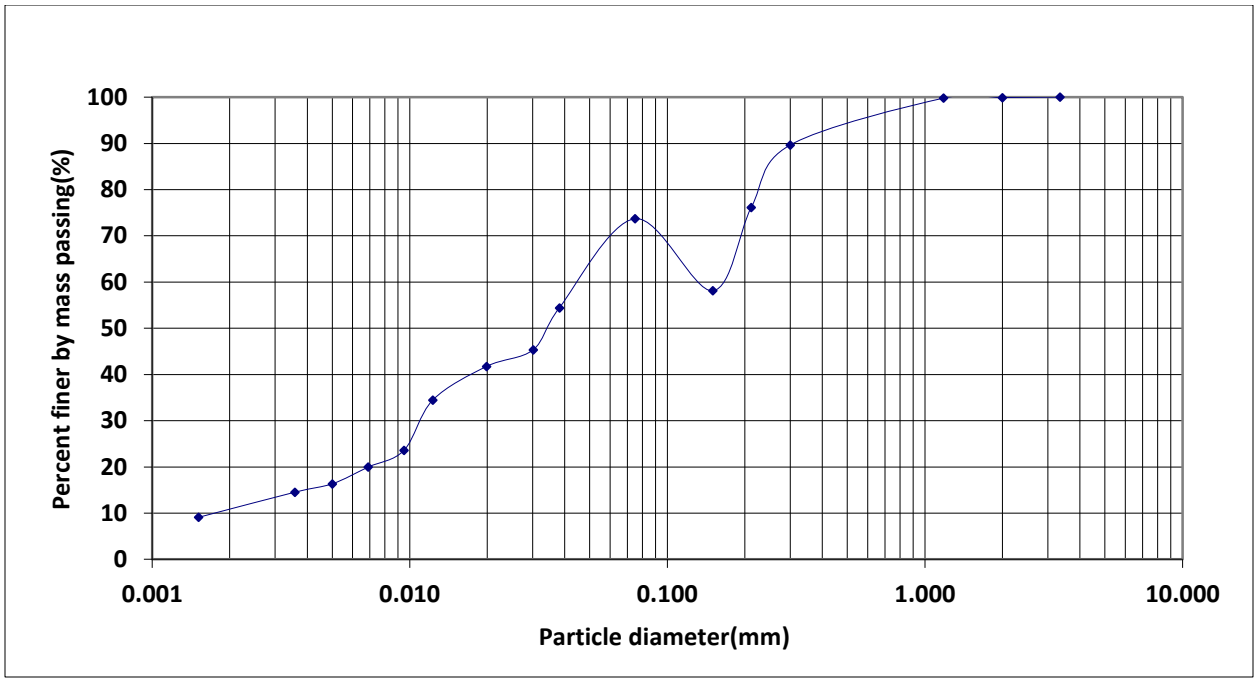


Figure 8-4 Particle size distribution curve – Irrigation Trial.

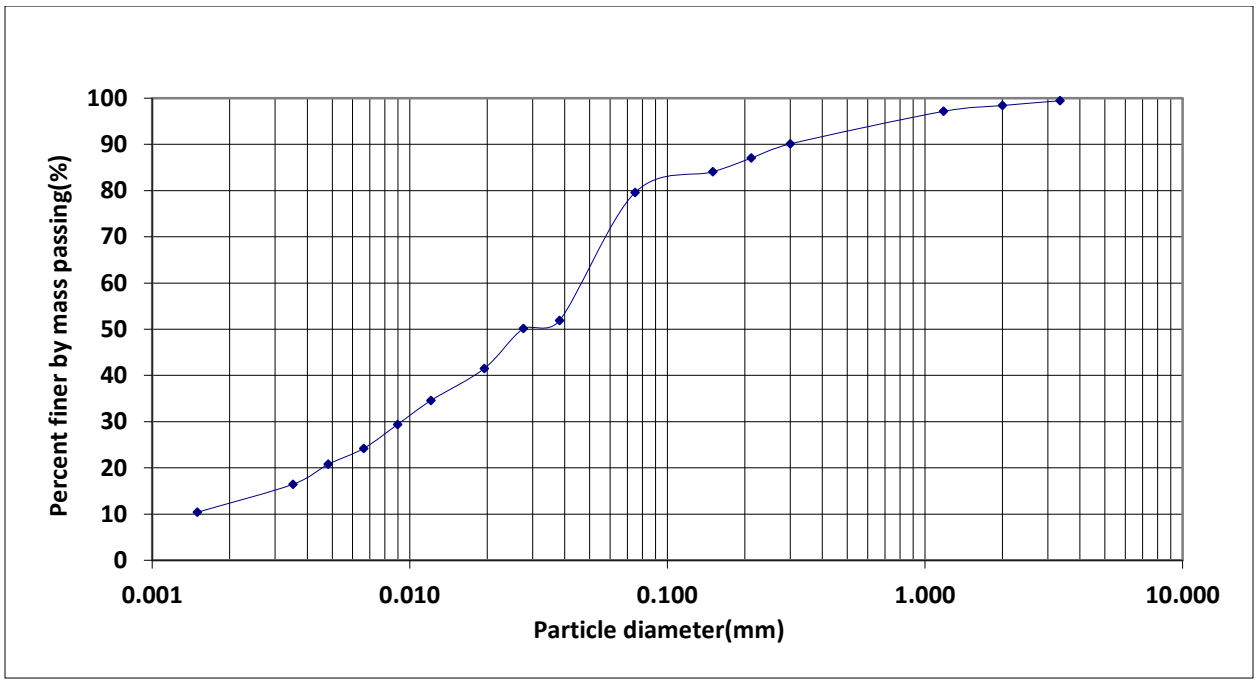


Figure 8-5 Particle size distribution curve – Grazing Trial.

B) Atterberg Limit Tests: Wet Sieving test

Table 8-1 Summary of geomechanical tests for soil classification. LL – liquid limit test; PL – plastic limit test; PI – plasticity index; SL – shrinkage limit test, and soil classification according to the Unified Soil Classification System - USCS.

Site	LL	PL	PI	SL	Soil Classification
Tiromoana Bush	35.24	36.07	-0.837	31.96	ML & OL non-plastic silt
The Willows Reserve	25.23	25.93	-0.71	24.52	ML & OL non-plastic silt
Dierickx Farm	35.32	31.85	3.47	27.71	ML & OL non-plastic silt
Irrigation Trial	41.46	29.54	11.92	23.75	M – silt
Grazing Trial	49.83	35.44	14.39	27.8	M – silt

8.2.2 Soil Chemical Analyses

Sample Type: Soil			
Test	**Method Description**	**Default Detection Limit**	**Samples**
Sample Registration*	Samples were registered according to instructions received.	-	1-27
Soil Prep (Dry & Grind)*	Air dried at 35 - 40°C overnight (residual moisture typically 4%) and crushed to pass through a 2mm screen.	-	1-27
pH	1:2 (v/v) soil:water slurry followed by potentiometric determination of pH.	0.1 pH Units	1-27
Olsen Phosphorus	Olsen extraction followed by Molybdenum Blue colorimetry.	1 mg/L	1-27
Available Nitrogen*	Determined by NIR, calibration based on Available N by Anaerobic incubation followed by extraction using 2M KCl followed by Berthelot colorimetry. (Calculation based on 15cm depth sample).	1 mg/L	1-27
Anaerobically Mineralisable N*	As for Available Nitrogen but reported as µg/g.	5 µg/g	1-27
Organic Matter*	Organic Matter is 1.72 x Total Carbon.	0.2 %	1-27
Total Carbon	Dumas combustion.	0.1 %	15
Total Nitrogen	Dumas combustion.	0.04 %	15
Total Carbon*	Determined by NIR, calibration based on Total Carbon by Dumas combustion.	0.1 %	1-14, 16-27
Total Nitrogen*	Determined by NIR, calibration based on Total N by Dumas combustion.	0.04 %	1-14, 16-27
Volume Weight	The weight/volume ratio of dried, ground soil.	0.01 g/mL	1-27

Figure 8-6 The following picture is a copy of the table displayed in the report provided by Hill Laboratories (Lab No: 1094338 v.1, 07/02/2013) which gives a brief description of the methods used to conduct the soil chemical analyses.

Table 8-2 Averages of soil chemical analysis performed on soil samples collected from the Rank Grass sites, in November-2012. Analyses performed by Hill Laboratories. For details on soil tests and interpretation of results see http://www.hill-laboratories.com/file/fileid/15530.

Sites	pH	P (mg/L)	Volume Density (g/mL)	Available N (kg/ha) - depth (15cm)	Anaerobically Mineralizable N (µg/g)
Tiromoana Bush	6.70 ± 0.44	5.50 ± 0.84	0.91 ± 0.06	167.17 ± 15.17	127.00 ± 2.68
The Willows Reserve	5.80 ± 0.32	7.00 ± 0.63	1.09 ± 0.06	79.50 ± 10.45	54.67 ± 4.76
Dierickx Farm	5.33 ± 0.88	8.33 ± 2.07	0.97 ± 0.07	96.33 ± 28.81	67.50 ± 23.87

Sites	Organic Matter (%)	Total Carbon (%)	Total N (%)	C/N Ratio	Mineralizable N/Total N (%)
Tiromoana Bush	6.32 ± 0.37	3.45 ± 0.32	0.37 ± 0.03	9.77 ± 0.47	3.37 ± 0.27
The Willows Reserve	3.13 ± 0.63	2.08 ± 0.37	0.21 ± 0.03	8.98 ± 0.17	2.18 ± 0.25
Dierickx Farm	6.20 ±1.32	3.60 ± 0.73	0.36 ± 0.07	9.98 ± 0.52	1.83 ± 0.27

Table 8-3 Averages of soil chemical analysis performed on soil samples collected from the Degraded Short Tussock sites, Mackenzie Basin, in November-2012. Analyses performed by Hill Laboratories. For details on soil tests and interpretation of results see http://www.hill-laboratories.com/file/fileid/15530.

Sites	pH	P (mg/L)	Volume Density (g/mL)	Available N (kg/ha) - depth (15cm)	Anaerobically Mineralizable N (µg/g)
Irrigation Trial	5.05 ± 0.08	8.33 ± 4.59	0.88 ± 0.05	94.33 ± 6.15	71.50 ± 7.06
Grazing Trial	5.27 ± 0.04	8.50 ± 0.82	0.98 ± 0.05	77.92 ± 10.78	53.67 ± 8.89

Sites	Organic Matter (%)	Total Carbon (%)	Total N (%)	C/N Ratio	Mineralizable N/Total N (%)
Irrigation Trial	7.82 ± 0.91	4.55 ± 0.52	0.43 ± 0.04	10.47 ± 0.36	1.67 ± 0.15
Grazing Trial	6.90 ± 1.52	4.03 ± 0.87	0.36 ± 0.05	10.98 ± 0.87	1.47 ± 0.17

"[…] the solution is not to throw in the towel and settle with the degraded alternatives. Rather, we should insist that humankind needs to rethink the way it is interacting with nature and find ways to avoid, minimize and (failing all else) to compensate for negative impacts." - Murcia, C., Aronson, J., Kattan, G. H., Moreno-Mateos, D., Dixon, K., Simberloff, D. (2014) A critique of the 'novel ecosystem' concept. Trends in Ecology and Evolution, 29(10), 548-553.